LEAF VENATION PATTERNS OF THE GENUS HIBBERTIA (DILLENIACEAE)[1]

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LEAF VENATION STUDIES have recently provided valuable taxonomic data about both fossil and living plants (Dilcher, 1974; Dolph, 1974; Hickey, 1973; Hickey & Wolfe, 1975; Mouton, 1970), although the venation patterns of leaves have long been neglected in taxonomic and descriptive studies (Foster, 1959). Hickey (1973) recognized the general neglect of various leaf characters in angiosperm systematics and noted the occurrence of incorrect generic assignments of fossil leaves which resulted from the consideration of superficial morphological characters only. He attributed this to the lack of a standardized system of leaf-character classification and responded by modifying and expanding the terminology of von Ettingshausen (1861) to devise a system of so-called leaf architectural classification (Hickey, 1973). Hickey (*loc. cit.*) felt that this classification system might serve as a valuable taxonomic tool, in view of the general consistency of the venation patterns in most dicotyledons. Both Hickey (1973) and Wolfe (1973) anticipated the value of such a classification in ecological and phylogenetic studies of woody dicotyledons, and Dilcher (1974) has stressed the importance of Hickey's classification scheme in evolutionary studies.

Early investigations concerning leaf venation were generally restricted to a single genus or species and often described the mature venation pattern with respect to its ontogeny (Foster, 1950a, b, 1951; Pray, 1954, 1955a, b, c, 1959; Ramji, 1961). More recently, comparative surveys of mature venation patterns in families and genera of dicotyledons have been presented (e.g., Dede, 1962; Vargheese, 1966; Sehgal & Paliwal, 1974). Hickey and Wolfe (1975), in a comprehensive synthesis of dicotyledonous leaf venation patterns, have utilized leaf architectural features to construct a synoptic key to dicotyledonous leaves following the subclasses of Cronquist (1968). However, the relative paucity of such studies emphasizes the need for further intensive surveys of leaf venation patterns in the systematic treatments of modern taxa.

The Dilleniaceae, a woody dicotyledonous family little studied since the taxonomic work of Gilg and Werdermann (1925), has been the subject of recent comparative morphological studies (Wilson, 1965, 1973; Dickison, 1967a, b, 1968, 1969, 1970a, b). This family is of particular interest since it is thought to occupy a key position with respect to angiosperm phylogeny (Dickison, 1967a). Stebbins (1974), for example, stated that the

Dilleniaceae is the most primitive extant family of angiosperms that exhibits a wide range of ecological preferences.

Hibbertia Andrews is the largest genus of Dilleniaceae and contains an estimated 150 species. These plants are mostly small, erect, much-branched shrubs under two meters tall, although some New Caledonian species reach a height of ten meters. Very few species are scandent, *H. dentata* and *H. scandens* being the only species which are clearly vines. Leaves are simple, of various shapes, and range from large to extremely small and scalelike. They are spirally arranged in all species except *H. coriacea* Baillon, which is endemic to Madagascar and has an opposite leaf arrangement. The leaves commonly have reflexed margins along with other xeromorphic specializations such as reduced size and stomatal crypts or grooves (Dickison, 1970a). Dense mats of trichomes are also commonly associated with the xeromorphic leaf forms.

Interpretations of inflorescence morphology among *Hibbertia* species vary. Hoogland (1951) reported that the inflorescences are dichasial and usually reduced to a few-flowered pseudo-raceme, spike, or solitary flower. Stebbins (1974, p. 264), however, stated that dichasia are not found in *Hibbertia*. The flower or inflorescence may be terminal or axillary, and the flowers are sessile or short-pedicellate. Flowers are conspicuous and usually have a yellow corolla composed of three to five members, although color may range from orange to white. Bracts and bracteoles are often present and may be poorly differentiated from the five, often bractlike sepals. Stamen number ranges from one to over 200, and the stamens may or may not be located along one side of the gynoecium. Staminodia are present in some species, and the stamens are either free or basally connate to form fascicles. Anthers dehisce longitudinally and introrsely or poricidally. The number of carpels ranges from one to five but may, occasionally, be greater (8–15 in *H. grossulariifolia*). They are free or basally connate and contain from 1–15 ovules borne upon a submarginal placenta. Styles are filiform and curved or recurved. The fruit is a follicle which dehisces along its inner suture to release 1–15 arillate seeds. On the basis of floral structure, *Hibbertia* is the most primitive genus in the family (Dickison, 1968).

The distribution of *Hibbertia* is latitudinally restricted between the equator and ca. 40° south latitude (van Balgooy, 1966). The genus is located primarily in Australia (including Tasmania), where approximately 125 species occur. Approximately 24 species are distributed in New Caledonia, and a single species occurs in both Madagascar (*H. coriacea*) and Fiji (*H. lucens*).

Hibbertia is found in lowland dunes, hills, and mountains up to 3000 meters in New Guinea. It also occurs in open forests, savannahs, or heaths, along rivers, and occasionally in bogs or in rain forests. It grows mostly on dry, sandy, or gravelly soil but is also known to inhabit loamy or clayey soils (van Balgooy, 1966).

The extraordinary diversity of *Hibbertia*, with respect to growth habit and floral structure, has been emphasized by Stebbins (1974). Dickison

(1970a) also commented upon the great anatomical diversity of the leaves, as well as on anatomical adaptations to extreme environmental conditions. Stebbins (1972, 1974) has illustrated how this genus provides, as does the entire family, a model to illustrate presumed adaptive radiation from intermediate habitats toward both more mesic and more xeric adaptations.

Recent workers (Hickey, 1971a, b; Hickey & Wolfe, 1975; Wolfe, 1973) have outlined relative levels of evolutionary specialization for leaf venation patterns in woody dicotyledons. If one assumes that venation patterns are indicative of various levels of phylogenetic advancement, an attempt to correlate these patterns with previously "established" phylogenetic trends in *Hibbertia* would be most informative. Positive correlations would serve to strengthen hypotheses regarding the organization of primitive and advanced leaf venation patterns in woody dicotyledons. Therefore, the objectives of this investigation are: (1) to describe the entire range of major and minor leaf venation patterns in *Hibbertia* Andr.; (2) to determine the consistency of venation patterns observed within the established sections and subsections of the genus; (3) to seek correlations between foliar venation patterns and evolutionary trends observed elsewhere in the plant body; and (4) to interpret such correlations, where possible, from an ecological and evolutionary perspective.

MATERIALS AND METHODS

Leaves of 97 species of *Hibbertia* Andr., representing all but one (Sect. V. OLIGOSTEMON) of the subgeneric sections of Gilg and Werdermann (1925), were studied. Leaves were cleared in 5 percent NaOH (Bailey & Nast, 1943), rinsed in water, and bleached in Stockwell's solution (Johansen, 1940). Cleared and bleached leaves were then rinsed in water, stained with 1 percent safranin, dehydrated through an ethanol series, and mounted on slides with balsam or permount mounting medium. Available stem material was prepared in the same manner in order to examine nodal anatomy in unsectioned material. A complete record of specimens examined, including their collection numbers and locations, is presented in *Appendix 1* of the original thesis (Rury, 1976). The cleared leaves examined in this study are located in the Cleared Leaf Collection, Division of Paleobotany, Smithsonian Institution (under the supervision of Leo J. Hickey, Curator), and in the collections of G. Ledyard Stebbins (University of California at Davis) and the present authors.

Illustrations of leaf venation were prepared using several techniques. Camera lucida drawings were made using a Wild dissecting microscope with a drawing attachment in order to illustrate accurately the basic and high order venation patterns of the leaf specimens. Negative prints of leaf venation patterns (see Dilcher, 1974) were prepared for several of the larger leaf specimens. In this technique, permanent slides of cleared specimens are used as negatives in a photographic enlarger to produce photographic (negative) prints of the venation patterns. Photomicrographs are also included to illustrate certain aspects of high order venation.

A limited number of specimens were paraffin-embedded and sectioned with a rotary microtome in order to study aspects of laminar anatomy.

For most species, numerous collections were examined to determine overall leaf size and morphology. Average leaf sizes were determined, in most cases, by measuring at least twenty leaves per species. Both young and mature leaves were measured to obtain a representative range of leaf size for each species studied. Published data of leaf sizes (Bentham, 1863; Hoogland, 1951; Hotchkiss, 1954; Willis, 1972) were also considered in assigning leaf size classes. Leaf size classes were designated according to the classification of Raunkiaer (1934): L. S. 1 — Leptophyll (up to 25 sq. mm.); L. S. 2 — Nanophyll (25 to 225 sq. mm.); L. S. 3 — Microphyll (225 to 2025 sq. mm.); L. S. 4 — Mesophyll (2025 to 18,222 sq. mm.).

For ease of comparison, species were considered in the taxonomic framework established by Gilg and Werdermann (1925) (APPENDIX 1). Leaf venation terminology follows, with necessary additions and modifications, the leaf architectural classification of Hickey (1973).

RESULTS

The great diversity of leaf venation patterns present within the genus *Hibbertia* can be conveniently arranged into a series of three basic types and nine subtypes. This leaf venation classification is based upon: (1) basic venation pattern; (2) details of basic venation pattern; (3) high order venation pattern; and (4) leaf size and nodal anatomy. The variability in leaf size and marginal configuration, as observed within several species of *Hibbertia*, emphasizes the necessity of careful collecting procedures in order to provide an accurate representation of the leaf morphology of any taxon.

TYPE I. SLENDER BROCHIDODROMOUS VENATION
     (e.g., PLATES III, F–I; IV, A, C, D, G; V, B; VI, G, I, K; XI, C).

Twenty-eight of the species examined possess a slender, weakly brochidodromous pattern designated as Type I venation. This type of leaf venation possesses slender or moderate secondary veins which generally follow a sinuous course and delimit intercostal areas of slightly irregular or relatively regular size and shape. Distinct intramarginal veins are lacking. High order venation may be lacking but is abundant in the leaves of most species. Leaves with sparse venation are reduced in size (L. S. 1, 2) and possess such xeromorphic features as a dense tomentum and revolute margins. The majority of species, however, possess abundant high order venation of the ramified, random reticulate type. Composite intersecondary veins are commonly formed by the anastomoses of admedially and transversely ramified tertiary veins. Intramarginal loop-forming veins are common in the leaves of most species and often enclose a random reticulum of veinlets. Marginal ultimate venation may be completely or in-

completely looped. Tertiary veins generally arise at wide acute angles from the secondaries and their brochidodromous arches and may ramify to form a random reticulum of indistinct vein orders (Types IB1 and IB2) or to form a system of large, polygonal "tertiary areoles" which exhibit no preferred orientation within the intercostal areas (Type IB3). Type IB3 leaf venation may also possess "pseudopercurrent" tertiary veins which are formed by transversely ramified veins that interconnect the secondary veins. Vein orders in all species are indistinct above the tertiary level, and areolation is generally incomplete and/or imperfect with freely terminating veinlets. These veinlets are simple or branched and may, as in the leaves of *H. huegelii*, possess terminal tracheoidal idioblasts. Leaves exhibiting polygonal tertiary areoles and occasional pseudopercurrent tertiaries are generally microphyllous in size, while leaves which lack these venation features are generally smaller in size, being leptophylls and nanophylls. All leaves are associated with trilacunar, three-trace nodes.

The slender, weakly brochidodromous vein pattern of *Hibbertia*, with numerous intramarginal loops and random reticulate high order venation, is similar to the leaf venation of the Magnoliidae, which has been described as "festooned brochidodromous" by Hickey and Wolfe (1975). The slight irregularity of the secondary veins, the random nature of the tertiary veins, and the occasionally poor distinction of tertiary veins from secondaries suggest that this Type I venation of *Hibbertia* is comparable to that of some plants with so-called second rank leaves (e.g., *Austrobaileya*) as described by Hickey (1971b).

TYPE I. . . . Slender, weakly brochidodromous venation lacking a strong, distinct pair of intramarginal veins. Low order venation is generally irregular or regular in its course. High order venation is generally ramified, random reticulate with poorly developed areolation.

1. High order venation is sparse or absent. Composite intersecondary veins are also sparse or absent. Leaves are reduced in size, being leptophylls or nanophylls (up to 225 sq. mm.) and often exhibiting xeromorphic features (i.e., dense pubescence, revolute margins). . . . . TYPE 1A.

    TRILACUNAR SPECIES: *H. stellaris.*
    UNILACUNAR SPECIES: *H. enervia, H. fasciculata,*
                           H. virgata.

1. High order venation present and generally abundant. Composite intersecondary veins are common. High order venation usually ramified, random reticulate with incomplete and/or imperfect areolation. Leaves of various sizes and with xeromorphic features in several species. . . . . TYPE IB.

  2. Percurrent and pseudopercurrent (transversely ramified) tertiary veins are absent. Tertiary and high order venation is random reticulate.

    3. Leaves mostly reduced in size, being leptophylls, nanophylls, or small microphylls (few spp.). . . . . TYPE IB1.

TRILACUNAR SPECIES: *H. diffusa, H. glaberrima,*
H. glomerosa, H. huegelii,
H. miniata, H. pachyrrhiza,
H. potentilliflora,
H. racemosa, H. salicifolia,
H. subvaginata.

UNILACUNAR SPECIES: *H. angustifolia, H. procumbens.*

3. Leaves not reduced in size, being microphylls (225–2025 sq. mm.).
.... TYPE IB2.

TRILACUNAR SPECIES: *H. amplexicaulis, H. cunninghamii,*
H. longifolia.

2. Percurrent tertiary veins absent. Pseudopercurrent, transversely ramified tertiary veins may be present. Ramified tertiary veins form a system of large, polygonal tertiary areoles. High order venation is random reticulate with incomplete and/or imperfect areolation with numerous freely terminating veinlets. Leaves are mostly microphylls or small mesophylls (225–18,222 sq. mm.). .... TYPE IB3.

TRILACUNAR SPECIES: *H. dentata, H. mylnei,*
H. nymphaea, H. perfoliata,
H. pilosa, H. saligna,
H. scandens, H. scandens var.
oxyphyllum, Hibbertia sp. 2.

TYPE II. STOUT BROCHIDODROMOUS VENATION
(e.g., PLATES I; II; V, G–I; VI, C–F, H, L–N; VII, C; VIII,
IX, A, B, D–G; X; XII, F–H).

Fifty-six of the species studied possess leaves that exhibit a stout, strongly brochidodromous venation pattern, arbitrarily designated as a Type II organization. Leaves of this type possess stout secondaries which follow a straight or sinuous course and delimit intercostal areas of irregular (Type IIA) or regular (Type IIB) size and shape. The arch segments of the brochidodromous secondaries are incorporated into a pair of stout, linear (Type IIA) or scalloped (Type IIB) intramarginal veins. The intramarginal veins of unilacunar species terminate basally as a massive accumulation of tracheary elements (see PLATES VIII, A, B, H; XIII, B), whereas those of the trilacunar species fuse with the lateral leaf traces within the leaf base. Species that lack abundant high order leaf venation are designated as Type IIA1 and are unique in their possession of "transversely composite intercostal veins." Such veins are formed by the anastomoses of a few secondary and tertiary veins that follow a longitudinal course proximal and parallel to the massive, primary midvein (e.g., *H. acicularis*). Leaves having this vein pattern are all reduced in size, being leptophylls or nanophylls, and exhibit xeromorphic features.

Most Type II species, however, possess abundant high order venation that forms a ramified, random reticulum of veinlets. Tertiary veins arise at wide acute to slightly obtuse angles, from the secondary veins and their

brochidodromous arches, and exhibit various ramifications which anastomose to form composite intersecondary veins within the intercostal areas. Loop-forming veins commonly enclose a system of admedially ramified veinlets. Marginal ultimate venation is generally incomplete but may form a completely looped, fimbrial, marginal ultimate vein as in the leaves of *H. cistifolia*. Areolation is generally incomplete in the reduced leaves of the unilacunar species. Leaves exhibit variously ramified tertiary and higher order veins which form a random reticulum of incomplete and/or imperfect areoles. However, the leaves of several New Caledonian species with scalloped intramarginal veins possess a nearly orthogonal reticulum of very well-developed, nearly perfect areoles (e.g., *H. lucens, H. wagapii*). Vein orders are generally indistinct above the tertiary or quaternary level, and freely terminating veinlets commonly range from simple to profusely branched as in *H. trachyphylla*. Veinlets are devoid of terminal, tracheoidal idioblasts. All leaves of Type IIA designation, with linear intramarginal veins, are reduced in size, possess xeromorphic features, and are associated with unilacunar, one-trace nodes. Leaves with Type IIB designation and scalloped intramarginal veins, however, may be nanophylls associated with unilacunar, one-trace nodes, or microphylls and mesophylls associated with trilacunar, three-trace nodal patterns.

The venation patterns considered here represent two relative levels of organization. Both species with linear intramarginal veins and those with scalloped intramarginal veins have relatively regular secondary veins and random reticulate high order venation with incomplete areolation. These leaf venation patterns could be considered comparable to the second rank leaves described by Hickey (1971b). The species with scalloped intramarginal veins and an orthogonal reticulum of well-developed areoles (e.g., *H. lucens, H. wagapii*), however, would be more comparable to the third rank leaves of Hickey (1971b) with respect to the greater regularity of their tertiary venation. The strong intramarginal veins of these species appear, as suggested by Hickey and Wolfe (1975) of *Hibbertia* and other dicotyledonous leaves, to have originated by the fusion and strengthening of the secondary brochidodromous arches. The festooned brochidodromous venation pattern, as observed in the Type I hibbertias and within the Magnoliidae (Hickey & Wolfe, 1975), is also evident in the more regular, stout venation of these hibbertias with scalloped intramarginal veins (Type IIB). The intramarginal veins of these hibbertias exhibit different degrees of linearity which may be considered as departures from the basically "scalloped" nature of the brochidodromous arch as represented in the weakly brochidodromous leaf venation of numerous hibbertias.

TYPE II. . . . Stout brochidodromous venation with a pair of stout, distinct, linear or scalloped intramarginal veins. Composite intersecondary veins may be present. High order venation, when present, forms a ramified, random reticulum or a nearly orthogonal reticulum with incomplete or moderately well developed areolation.

1. Strong, linear intramarginal veins are present which generally terminate basally in the lamina as a mass of tracheary elements or an anastomosis of veinlets. Secondary veins are regular or irregular in their course, generally delimiting intercostal areas of irregular size and shape. TYPE IIA.

   2. High order venation sparse or absent. Composite intersecondary veins are also absent. "Transversely composite intercostal veins" are formed by secondary and a few tertiary vein anastomoses. Areolation is lacking or incomplete and poorly developed, with few high order veins. Leaves are reduced in size, being leptophylls or nanophylls with xeromorphic features. .... TYPE IIA1.

      UNILACUNAR SPECIES: *H. acicularis, H. cistiflora, H. elata, H. exutiacies, H. stricta.*

   2. High order venation abundant, composite intersecondary veins are present, and "transversely composite intercostal veins" are absent. High order venation is ramified, random reticulate. Areolation is either incomplete and poorly developed or is nearly complete and moderately well developed. Leaves are reduced in size, being leptophylls or nanophylls usually with xeromorphic features. .... TYPE IIA2.

      UNILACUNAR SPECIES: *H. aurea, H. gracilipes, H. hypericoides, H. microphylla, H. mucronata, H. pedunculata, H. pungens, H. rhadinopoda, H. stirlingii, H. tomentosa, H. uncinata, H. vestita.*

1. Strongly brochidodromous venation with a pair of stout, distinct, scalloped intramarginal veins which, in the trilacunar species, fuse basally with the lateral leaf traces. These intramarginal veins may, in the unilacunar species, terminate freely and massively within the leaf base. The trilacunar species have leaves with three leaf traces which remain distinct and unfused for several millimeters within the leaf base. The low order (2°) veins are generally very regular, delimiting intercostal areas of regular size and shape. Composite intersecondary veins are common. Pseudopercurrent, transversely ramified tertiary veins are occasionally present. High order venation is ramified, random reticulate or may be nearly orthogonal reticulate. Areolation is imperfect and nearly incomplete or is well developed and nearly perfect, often with numerous freely ending veinlets. Leaves are of various sizes, but are mostly nanophylls, microphylls, or small mesophylls. The smallest leaves are generally associated with unilacunar nodal patterns. .... TYPE IIB.

      TRILACUNAR SPECIES: *H. altigena, H. baudouinii, H. brongniartii, H. coriacea, H. dealbata, H. deplancheana, H. ebracteata, H. heterotricha, H. inconspicua, H. lucens, H. lucida, H. nana, H. ngoyensis, H. oubatchensis, H. pancheri, H. patula, H. podocarpifolia, H. pulchella, H. scabra,*

H. tontoutensia, H. trachyphylla, H. vanieri,
H. virotii, H. wagapii, Hibbertia sp. 1,
Hibbertia sp. 3.

UNILACUNAR SPECIES: H. aspera, H. asterotricha, H. bracteata,
H. cistoidea, H. cistifolia, H. furfuracea,
H. hermanniifolia, H. hexandra,
H. melhanoides, H. nitida, H. oblongata,
H. sericea, H. silvestris.

TYPE III. CRASPEDODROMOUS VENATION
(e.g., PLATES IV, E, F; VI, A; VII, B, D; IX, C; XI, A, B).

Craspedodromous leaf venation occurs in only thirteen of the species examined. All but one of these species possess either a semicraspedodromous or a mixed craspedodromous venation pattern which is associated with a toothed or half-toothed leaf margin. The craspedodromous condition appears, in most cases, to be the result of an ontogenetic modification of the weakly brochidodromous pattern. Semicraspedodromous venation has apparently resulted from the formation and subsequent vascularization of marginal teeth in leaves with weakly brochidodromous venation. The tooth vasculature arises exmedially from the brochidodromous arch in leaves of *Hibbertia cuneiformis, H. linearis, H. linearis* var. *obtusifolia*, and *H. serrata*. This ontogenetic transition will be considered in more detail later. Such a morphological leaf dimorphism of entire-margined young leaves and toothed older leaves has been illustrated for *H. serrata* by Hotchkiss (1954); a similar example is illustrated for *H. linearis* var. *obtusifolia* in PLATE XI, A.

As in the leaves of species with weakly brochidodromous venation, semicraspedodromous leaves also possess slender or moderate secondary veins which diverge from a moderate midvein at moderately acute angles and follow a sinuous and recurved (*H. montana* var. *major*) or curved (*H. linearis* var. *obtusifolia*) course, delimiting intercostal areas of relatively irregular size and shape which commonly enclose composite intersecondary veins. Abundant loop-forming veins arise exmedially from the brochidodromous arches and form a festooned brochidodromous vein pattern similar to that of the species with entire leaf margins and a Type I venation pattern. Occasional pseudopercurrent tertiary veins can be found, and a system of large, polygonal "tertiary areoles," with no preferred orientation within the intercostal areas, may occur. Tertiary areoles are subdivided into a random reticulum of admedially and transversely ramified veinlets. There may also be ramified high order veins within the intramarginal loops. High order venation of the semicraspedodromous leaves is essentially identical to that of the weakly brochidodromous, Type I leaves of several species of *Hibbertia*. Marginal ultimate venation is generally incompletely looped and may be of tertiary or quaternary origin. Areolation is generally incomplete and/or imperfect and ramified, with freely ending veinlets that may bear terminal idioblasts (e.g., *H. linearis* var. *obtusifolia*).

Simple craspedodromous venation was observed only in the immature and mature leaves of *H. grossulariifolia*. This species possesses moderate, nearly straight secondaries which diverge from the moderate midvein at consistently moderate acute angles, delimit intercostal areas of very uniform size and shape, and terminate in marginal teeth of the dillenioid type (*sensu* Hickey & Wolfe, 1975). Composite intersecondaries arise via admedially ramified tertiary veins which in turn originate, admedially, from geniculate, transversely ramified ("pseudopercurrent") tertiaries. Large, polygonal tertiary areoles of non-preferred orientation are subdivided, by variously ramified high order veins and veinlets, into a random reticulum of incomplete areoles. Numerous freely ending veinlets with terminal idioblasts are common. With respect to high order venation, the leaves of *H. grossulariifolia* are very similar to the majority of plants with semicraspedodromous and weakly brochidodromous venation.

The mixed craspedodromous venation pattern is present in *H. banksii* and *H. holtzei*. In the mature leaves of *H. banksii*, this pattern appears to be the result of an ontogenetic transition from a weakly brochidodromous condition. Young leaves of *H. banksii* have an entire margin and a weakly brochidodromous venation pattern with a nearly orthogonal reticulum of very well-developed, small, quadrangular areoles. Larger, more mature leaves, however, have an entire margin and a weakly brochidodromous pattern only within the basal half of the lamina. The upper half of the lamina possesses a crenate margin that is associated with vein termini from several simple craspedodromous secondary veins. The high order venation exhibits an identical pattern in both the immature and mature leaves of *H. banksii*. The ontogenetic change in basic venation pattern is illustrated in PLATE VII, B, D. The areolation of leaves of *H. banksii* represents the highest level of development in *Hibbertia* and is comparable to that of *Hibbertia* sp. 1 (PLATE XV, C), a species to which it is believed to be closely related (Stebbins, 1975, pers. comm.). Freely ending veinlets and terminal tracheoidal idioblasts are absent in the leaves of *H. banksii*.

The mixed craspedodromous leaves of *H. holtzei* possess a basal eucamptodromous pattern and an apical simple craspedodromous pattern. The leaf is crenate along its upper half, with hydathodal crenations supplied directly by the simple craspedodromous secondary veins. Basal, upcurving eucamptodromous secondary veins follow a sinuous, tapering course and form a series of intramarginal loops along the exmedial sides of the tenuous, superadjacent secondary veins. Composite intersecondary veins and large, polygonal tertiary areoles with non-preferred orientation are formed by admedial and transverse tertiary vein ramifications. The tertiary areoles are subdivided into a random reticulum of high order veins and veinlet termini. Percurrent tertiary and pseudopercurrent tertiary veins are common, the former being most abundant between the basal, eucamptodromous secondary veins. Tertiary veins generally arise at right angles but may arise at wide acute or slightly obtuse angles. Loop-forming veins are numerous and form up to five (2° to 6°) orders of intramarginal loops which commonly enclose a random reticulum of ad-

medially ramified, high order veinlets. Marginal ultimate venation is mostly completely looped and of quaternary or quintary origin. Vein orders are indistinct above the tertiary level and are variously ramified into a random reticulum of imperfect, moderately well-developed areolation. Simple or slightly branched, freely terminating veinlets are commonly devoid of terminal idioblasts.

The leaves of all craspedodromous species are microphylls or mesophylls and are associated with trilacunar, three-trace nodes. The three leaf traces may remain distinct and unfused within a sessile leaf base (semicraspedodromous species) or may fuse within the base of a laminar (*H. grossulariifolia*) or terete (*H. banksii, H. holtzei*) petiole to form a single primary midvein. The leaves of species with these three types of craspedodromy appear to correspond to a level of structural organization slightly below the third rank condition as described by Hickey (1971b).

TYPE III. . . . Leaves with craspedodromous venation patterns. Secondary veins generally follow a straight or irregularly sinuous course and delimit intercostal areas which are relatively regular in size and shape. Secondary veins are occasionally interconnected by pseudopercurrent, transversely ramified tertiary veins. High order veins form a ramified, random reticulum with incomplete and/or imperfect areolation. High order venation may also form a nearly perfect system of small, quadrangular areoles (*H. banksii*). Leaves are large nanophylls, microphylls, or small mesophylls. . . . . 1.

1. Basic venation pattern is semicraspedodromous or mixed craspedodromous with vascularized marginal teeth, at least along the upper half of the leaf margin. An ontogenetic change from a weakly brochidodromous vein pattern is evident in the species with a semicraspedodromous, mature venation pattern. High order venation is generally ramified, random reticulate with incomplete areolation. High order venation may be more nearly orthogonal reticulate with moderately developed (*H. holtzei*) or well-developed areolation (*H. banksii*). . . . . TYPE IIIA.

> TRILACUNAR SPECIES: *H. banksii, H. cuneiformis, H. gilgiana,*
> *H. holtzei, H. lasiopus, H. linearis,*
> *H. linearis* var. *obtusifolia, H. montana,*
> *H. montana* var. *major, H. quadricolor,*
> *H. serrata, H. tetrandra.*

1. Basic venation pattern is simple craspedodromous throughout ontogeny. Secondary veins are straight and regular, and delimit intercostal areas of regular size and shape. Marginal teeth are directly vascularized by these secondaries. Pseudopercurrent tertiary veins are present. High order venation is ramified, random reticulate with incomplete and imperfect areolation. . . . . TYPE IIIB.

> TRILACUNAR SPECIES: *H. grossulariifolia.*

DISCUSSION

ONTOGENETIC TRANSITIONS.

Ontogenetic changes in basic leaf venation pattern are apparent in several species of *Hibbertia*. Weakly brochidodromous patterns are associated with entire margins in all species examined. However, in several species entire margins and an associated weakly brochidodromous venation are confined to the smaller leaves. More mature, larger leaves possess a toothed margin and a semicraspedodromous venation pattern which apparently results from the formation of marginal teeth vascularized by veins arising exmedially from the slender brochidodromous, secondary arches of the developing leaves. The resultant semicraspedodromous venation pattern is identical to the weakly brochidodromous leaf venation exhibited by the juvenile foliage in all respects except the vascularized, marginal teeth. It remains unclear whether the apparent ontogenetic transition of leaf morphology and venation occurs within a single leaf or within series of successively younger leaves along the branches of these plants; further studies are clearly necessary.

However, the marginal ultimate venation of several species with weakly brochidodromous venation indicates that this "transition potential" may reside within individual leaves. Leaves of *H. amplexicaulis*, *H. cunninghamii*, and *H. perfoliata* have massive tracheary accumulations within their marginal ultimate venation adjacent to scarcely noticeable marginal bulges (see PLATE XIV, D). These tracheary masses are considered by Stebbins (1976, pers. comm.) to be identical to the tooth vasculature of the dentate-leaved hibbertias. These tracheary accumulations may represent a "pre-tooth" and thus may indicate a potential of several species to form toothed leaf margins. The occurrence of marginal teeth in open, semi-xeric habitats seems to favor this hypothesis since marginal teeth do not seem to be disadvantageous in these drier areas, but may simply represent an ontogenetic development in response to periodic rainfall and ephemerally moist conditions.

Another possibility is to consider these tracheary accumulations as relictual teeth. Since the species exhibiting this feature are inhabitants of mesic regions, there seems to be no obvious active selective pressure which would favor the loss of marginal teeth. Hence, if these structures are, indeed, relictual teeth, it might be reasonable to postulate a recent migration of these species from a dry region into more mesic habitats.

Leaves of *Hibbertia banksii* apparently represent a different type of ontogenetic change in basic venation pattern. The young leaves of this species possess a weakly brochidodromous vein pattern with tertiary and high order veins that are poorly distinguished from one another and from the secondary veins. The transition, in the upper half of the leaf, from this weak brochidodromy to simple craspedodromy apparently results from a differential thickening of high order veins which connect the basal portion of the brochidodromous secondary arch with the marginal tooth.

The arch segments in the upper half of the leaf evidently become "de-emphasized" with respect to their development and become part of the high order, intercostal vein reticulum. Apparently, an extension of the secondary vein develops from high order veins and connects the base of the brochidodromous arch with the marginal crenation to form a simple craspedodromous secondary vein. Such a "shift" in vein development is responsible, in many dicot leaves, for ontogenetic transitions from semi-craspedodromy to simple craspedodromy (Hickey, 1975, pers. comm.). As in the ontogenetic transitions observed in other species, the high order venation of leaves of *H. banksii* remains unchanged throughout their ontogeny. This evidence seems to indicate a morphological continuum between the weakly brochidodromous and the craspedodromous venation patterns which appears to be ontogenetically and developmentally traversed by the leaves of several species of *Hibbertia*.

The relationship between the formation and vascularization of marginal teeth or denticulations is of great interest both developmentally and physiologically. The occurrence of marginal "pre-teeth," as in the leaves of *H. amplexicaulis*, *H. cunninghamii*, and *H. perfoliata*, suggests a possible hormonal mechanism in the "co-formation" of marginal teeth and tooth vasculature. Massive tracheary accumulations are often found within protuberant leaf apices (see PLATE XV, A), as in the marginal teeth, and suggest a possible apical growth for the marginal teeth. Two preliminary hypotheses of hormonal activity at these sites of tooth formation may warrant further investigation: (1) acropetal transport of a tooth-formation stimulus from the vascular aggregations; and (2) basipetal transport of a vascularization stimulus from the meristematic, marginal tooth apex. The presence of a massive accumulation of tracheary tissue not associated with a marginal tooth in the leaves of several species (e.g., *H. cunninghamii*) would seem to favor the former hypothesis. A detailed developmental-physiological investigation is needed to confirm or negate these hypotheses.

NODAL ANATOMY, LEAF SIZE, AND LEAF ATTACHMENT.

Nodes of *Hibbertia* are either trilacunar, three-trace, or unilacunar, one-trace. Sixty-two species studied possess trilacunar, three-trace nodes, and such nodes usually occur in species with sessile leaves. Fifty-one of these trilacunar species have leaves that are either microphyllous or mesophyllous in size. Furthermore, the majority of these species have three unfused leaf traces within a sessile leaf base. This correlation between leaf size and nodal pattern is not absolute, however, since species with reduced leptophyllous or nanophyllous leaves do, occasionally, possess trilacunar, three-trace nodes (e.g., *H. diffusa*). Eleven of the trilacunar species examined have reduced, leptophyllous or nanophyllous leaves, but most of the species examined that possess reduced leaves lack a trilacunar, three-trace nodal pattern. Trilacunar, three-trace nodes are considered to be the primitive, or generalized, condition in *Hibbertia* and the entire family Dilleniaceae (Dickison, 1969; Stebbins, 1972). The occurrence of

this generalized nodal pattern in the majority of species is not unusual since *Hibbertia* is the most primitive or generalized genus of the entire family Dilleniaceae with respect to other morphological features (viz., large flowers with spirally arranged parts and free carpels, primitive wood anatomy, and sessile leaves with relatively unspecialized venation patterns (Dickison, 1967a, 1968)). The frequent association of trilacunar nodes with unfused leaf traces within the sessile bases of relatively large leaves suggests that nodal anatomy, leaf size, and leaf attachment may represent a complex of characters that have closely interrelated and interdependent character states.

Trilacunar nodes are also found in association with clasping, sheathing, or perfoliate leaf bases in *H. amplexicaulis*, *H. nymphaea*, and *H. perfoliata*, the leaves of which are all microphylls and exhibit weakly brochidodromous venation patterns.

Several species of *Hibbertia* also possess petiolate microphylls or mesophylls that are associated with trilacunar, three-trace nodes. The leaf traces fuse within the base of the laminar (*H. grossulariifolia*) or terete (*H. coriacea*, *H. dentata*) petiole to form a single primary midvein. The petiolate condition probably represents a morphological advancement since it is observed in the more advanced, trilacunar (*Tetracera*) and multilacunar (*Davilla*, *Dillenia*) genera of Dilleniaceae, all of which also have relatively large, microphyllous or mesophyllous leaves (Dickison, 1969). Mutilacunar nodes, which in the Dilleniaceae are considered to be derived from the primitive, trilacunar condition (Dickison, 1969), are strongly correlated (100 percent) with large leaf sizes and the presence of petioles.

Thirty-five of the species examined possess unilacunar, one-trace nodes that are generally associated with sessile leaves. Nearly all of these unilacunar species also have reduced, leptophyllous or nanophyllous leaves. A strong reciprocal correlation is evident in that ca. 74 percent of the species with reduced leaves also possess unilacunar, one-trace nodal patterns. These correlations are a reflection of the relationship between leaf size and nodal anatomy in *Hibbertia*. A similar correlation is apparent in the dilleniaceous genus *Pachynema*, which illustrates the same association of reduced, scalelike leaves with unilacunar, one-trace nodal patterns. The reduction in leaf size and nodal structure has been considered a specialization within the Dilleniaceae, derived from the generalized, trilacunar condition (Dickison, 1969; Stebbins, 1972).

Venation patterns of the laminar base are also related to nodal structure, regardless of leaf size. In trilacunar species with both weakly and strongly brochidodromous leaf venation, the basal secondary veins often diverge from the lateral leaf traces within the sessile leaf base (e.g., *H. gilgiana*, *H. virotii*). The unilacunar species of *Hibbertia* generally possess reduced leaves with strongly brochidodromous venation and stout, linear (Type IIA) or scalloped (Type IIB) intramarginal veins which terminate massively within the sessile leaf bases on either side of the single massive midvein (see PLATES VI, H; VIII, A, H; XIII, B). The intramarginal vein termini remain distinct from the midvein and may anasto-

mose with numerous veins and veinlets to form a dense, basal reticulum of tracheary elements as in *H. sericea*. Such basal intramarginal vein termini are always associated with unilacunar, one-trace nodes, regardless of leaf size. The structural and physiological significance of these massive vein termini is uncertain.

LEAF VENATION IN RELATION TO THE SYSTEMATICS OF HIBBERTIA.

Sections TRISEMA, POLYSTICHE, SPICATAE, subsection TRIMORPHANDRA of sect. CYCLANDRA, and several species of uncertain taxonomic position are exclusively New Caledonian or Fijian in distribution. All of these New Caledonian and Fijian species possess large leaves, trilacunar, three-trace nodes, and a remarkably similar, strongly brochidodromous Type IIB venation pattern. These species differ only with respect to their high order venation, which may be distinctly ramified and random reticulate with incomplete areolation (e.g., *H. lucida, H. trachyphylla*), or less distinctly ramified and nearly orthogonal reticulate with very well-developed areolation as in the leaves of *H. lucens* and *H. wagapii*. Terminal idioblasts are lacking in the leaves of all New Caledonian and Fijian hibbertias, and the species groupings (*sensu* Gilg & Werdermann, 1925) appear to be quite natural on the basis of vegetative morphology. On the basis of both leaf venation and floral morphology (see APPENDIX 1), however, subsect. TRIMORPHANDRA would be more naturally placed in one of these New Caledonian sections than in the Australian section CYCLANDRA.

Section CYCLANDRA, which is primarily Australian except for the aforementioned New Caledonian subsect. TRIMORPHANDRA, represents a very heterogeneous assemblage of leaf venation patterns (see TABLE 1). This section includes those hibbertias with the most generalized leaf venation, as well as the most generalized floral structure, within the genus (see APPENDIX 1). Both unilacunar and trilacunar species are present and are associated with either normal sized (L. S. 3, 4) or reduced leaves (L. S. 1, 2). Seventeen species possess leaves with a weakly brochidodromous venation pattern, whereas fourteen species exhibit strongly brochidodromous leaf venation. Craspedodromous leaf venation occurs in only seven of the species examined from this section, the majority of which exhibit the semicraspedodromous pattern.

Several of the subsections of CYCLANDRA, however, exhibit a relatively homogeneous assemblage of leaf venation patterns (TABLE 1). All seven species examined from subsect. TOMENTOSAE, for example, possess leaves with strongly brochidodromous venation. Subsection HEMIHIBBERTIAE is somewhat less homogeneous; the leaf venation of eight of the twelve species examined is weakly brochidodromous; that of the other four species is either strongly brochidodromous or craspedodromous. However, considering the similarity of the weakly brochidodromous and semicraspedodromous leaf venation patterns, the total array of venation patterns within this subsection is relatively homogeneous. Subsection SUBSESSILES represents the most heterogeneous grouping as evidenced by the presence of four different leaf venation patterns (see TABLE 1). Subsection BRAC-

TABLE 1. Distribution of venation types among sections of the genus Hibbertia (sensu Gilg & Werdermann, 1925).*

SECTION	VENATION TYPES								
	IA	IB1	IB2	IB3	IIA1	IIA2	IIB	IIIA	IIIB
TRISEMA							+		
POLYSTICHE							+		
SPICATAE							+		
CYCLANDRA	+	+	+	+	+	+	+	+	+
FASCICULATAE	+	+							
BRACTEATAE	+	+						+	
SUBSESSILES		+		+	+			+	
BRACHYANTHERAE	+					+			
VESTITAE						+			
TOMENTOSAE						+	+		
HEMIHIBBERTIAE		+	+	+			+	+	+
TRIMORPHANDRA							+		
SALICIFOLIAE		+							
CANDOLLEA	+	+				+		+	
HEMIPLEURANDRA						+	+		
HEMISTEMMA		+					+	+	
PLEURANDRA		+			+	+	+		
Uncertain				+			+	+	

* Based on the examination of 97 species.

TEATAE, on the other hand, is a relatively homogeneous grouping having consistently weakly brochidodromous leaf venation or a slight modification thereof. Subsections FASCICULATAE, BRACHYANTHERAE, and VESTITAE, each with few species, are also relatively uniform with respect to leaf morphology.

Most species of the section CANDOLLEA have leaf venation patterns of the weakly brochidodromous type and possess trilacunar, three-trace nodes. This section thus represents a natural species grouping on the basis of both vegetative and floral morphology (see APPENDIX 1).

Sections HEMIPLEURANDRA and PLEURANDRA are very homogeneous with respect to leaf venation patterns and include species with uniformly unilacunar, one-trace nodes and reduced leaves with strongly brochidodromous venation patterns. All of the species studied also have basal intramarginal vein termini (see PLATE VII, A, H).

Hibbertia section HEMISTEMMA includes a relatively heterogeneous array of leaf venation patterns with strongly brochidodromous venation (*H. coriacea, H. dealbata, Hibbertia* sp. 1), mixed craspedodromous venation (*H. banksii, H. holtzei*), and reduced leaves with weakly brochidodromous venation (*H. angustifolia*). The single character state common to all species of this section except *H. angustifolia* is the well-developed high order venation with nearly complete areolation.

It can be concluded that, with few exceptions, the subgeneric groups

established by Gilg and Werdermann (1925) on the basis of floral morphology generally represent natural associations with respect to the homogeneity of vegetative characters and leaf venation patterns.

EVOLUTIONARY TRENDS.

Relative levels of specialization of the foliar venation of woody dicotyledons have been determined through comparative morphological studies of both fossil and extant dicot leaves (Hickey, 1971b; Wolfe, 1973; Hickey & Wolfe, 1975). General trends of specialization are represented by: (1) an increase in regularity of both low and high order venation; (2) a shift from vein orders which are indistinct to successive vein orders which are readily distinguished from one another; (3) a shift from tertiary venation which is random to that which is very regular, often with rigidly percurrent veins traversing the intercostal areas; and (4) a progressive development from random, incomplete areolation to orthogonal, well-developed (perfect) areolation. The different levels of leaf venation specialization in woody dicots have been called "ranks" by Hickey (1971b) and may be outlined as follows. First rank leaves have secondary veins that follow an irregular course and delimit intercostal areas that lack uniform size and shape. Second rank leaves possess secondary veins that are relatively regular in their course, intercostal areas of generally uniform size and shape, and random tertiaries that are frequently not well differentiated from the secondaries. Third rank leaves exhibit more organized venation, with tertiaries of relatively consistent course and areoles of random size or placement. Fourth rank leaves are further specialized, with areoles of uniform size and shape that are regularly arranged within the intercostal areas.

Several of the above levels, or "ranks," of leaf venation specialization occur in *Hibbertia*. The basic venation pattern of all species is pinnate brochidodromous or craspedodromous and, thus, may be considered as generally primitive (*sensu* Hickey & Wolfe, 1975) in comparison to woody dicotyledons as a whole. Simple leaves with entire margins, as present in most species of *Hibbertia*, are considered the primitive leaf type in woody dicots (Hickey & Wolfe, 1975).

Species of *Hibbertia* with weakly brochidodromous leaf venation and random reticulate high order venation represent the least specialized venation in the genus and also in the entire family Dilleniaceae. The relative irregularity of the secondary veins, the intercostal areas, and the high order venation is that of the first, or in some cases (e.g., *H. amplexicaulis*) second rank leaves (*sensu* Hickey, 1971b). The irregular venation of such Type IB1 leaves (e.g., *H. glaberrima, H. glomerosa*) presents the most probable condition for the leaf venation of the ancestral Dilleniaceae. Approximately 30 percent of the species studied occur in mainland Australia (including Tasmania) and have such first or low second rank leaf venation.

Leaves of *Hibbertia* with strong, regular brochidodromous venation with distinct intramarginal veins and ramified, random reticulate or nearly or-

thogonal reticulate (e.g., *H. lucida, H. wagapii*) high order venation exhibit second or third rank organization (*sensu* Hickey, 1971b).
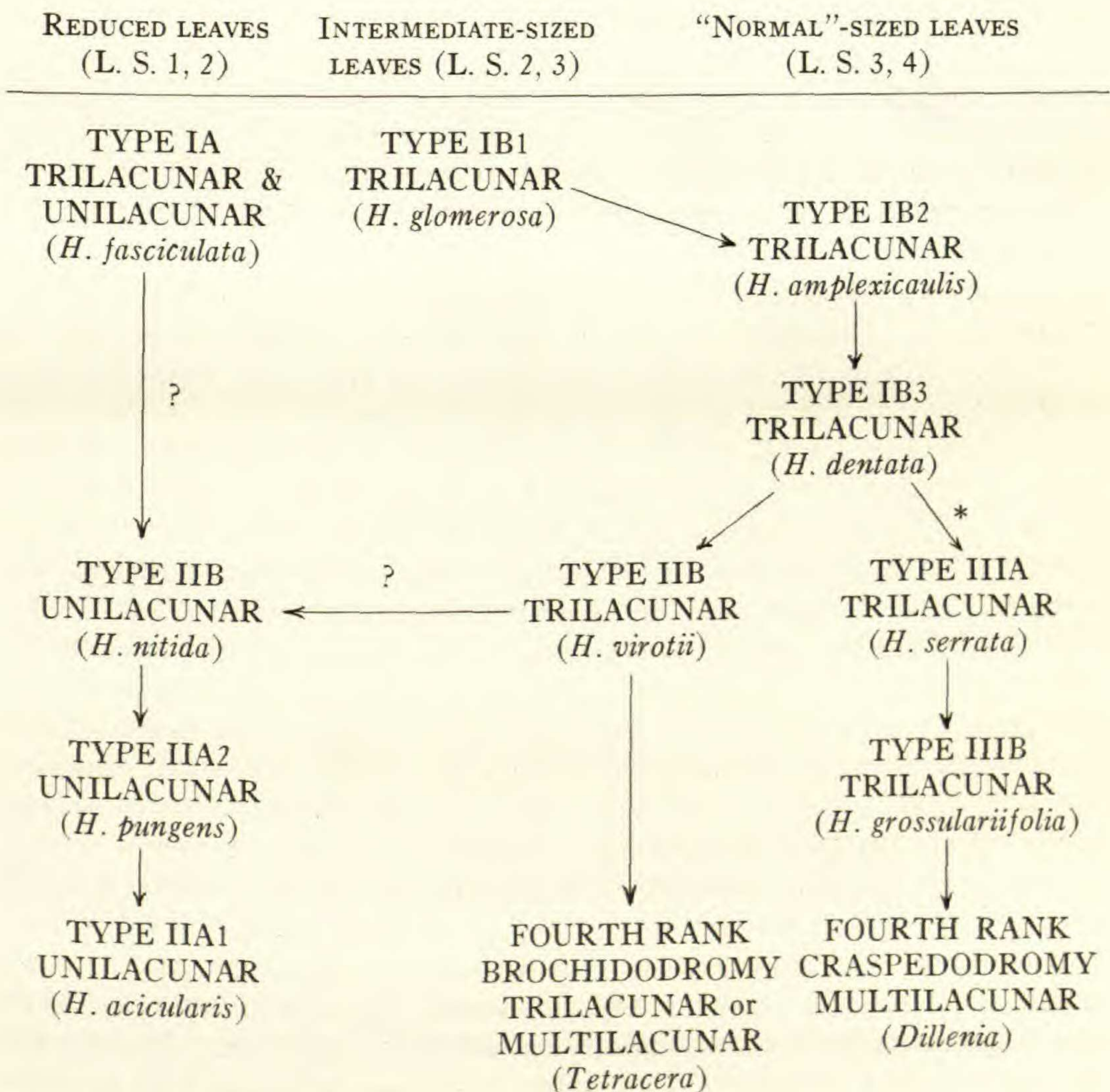
Craspedodromous species of *Hibbertia* are more specialized than the brochidodromous species with respect to their toothed marginal configuration, which is regarded as an advanced feature. However, the majority of these species have vein patterns that are no more advanced than those of species with weakly brochidodromous venation. Most craspedodromous hibbertias have a semicraspedodromous venation of first or second rank organization. The mixed craspedodromous leaves of *H. banksii* and *H. holtzei*, however, are considerably more advanced than the semicraspedodromous species with respect to their high order venation. *Hibbertia banksii* has a well-developed system of small, quadrangular areoles, a condition which is lacking in species with a semicraspedodromous venation. Leaves of *H. holtzei* have a moderately specialized system of high order venation that contains several percurrent tertiary veins and a moderately well-developed system of areoles. The simple craspedodromous leaves of *Hibbertia grossulariifolia* are advanced over most hibbertias with respect to their crenate margins. The regularity of the secondary veins and of the intercostal areas of this species represents a basic vein pattern which is more specialized than that of species with a weakly brochidodromous condition. The high order veins, however, with the exception of a few weakly percurrent tertiary veins, are organized into a ramified, random reticulum of incomplete areoles which is no more advanced than in other species.

Hibbertia has the least specialized leaf venation in the Dilleniaceae. All other genera in the family, except the xerophytic genus *Pachynema*, have a very regular eucamptodromous-brochidodromous, brochidodromous, or simple craspedodromous venation pattern with a moderately or well-developed system of rigidly percurrent tertiary venation and oriented, nearly perfect, or perfect areolation. Rigidly percurrent tertiary venation and oriented, well-developed areolation are lacking in all hibbertias. Hickey (1971a) has observed that variations from the basic venation pattern within a family may appear in disjunct genera or in genera that are found in environments atypical of the remainder of the family. Most genera of Dilleniaceae inhabit mesic, everwet parts of the tropics (Hoogland, 1951), whereas *Hibbertia* favors habitats that range from xeric to mesic-hydric with numerous species inhabiting semi-xeric regions. The apparent "regression" to a lower level of foliar venation in numerous needle-leaved species of *Hibbertia*, as compared to the other second and third rank hibbertias, presents an excellent example of Hickey's observation. A similar situation is illustrated by the genus *Pachynema*, which is usually regarded as an extreme xeromorphic derivative of *Hibbertia* and exhibits a "regression" of leaf venation specialization below the level characteristic of *Hibbertia* and all other Dilleniaceae. Hickey's (1971b) contention that plants native to arctic, alpine, and arid environments may also show such a regression is supported by evidence from the xeric species of *Hibbertia* and the xeric genus *Pachynema*. In dealing with taxa of extreme habitats, however, great difficulty is encountered in assigning relative levels of specializa-

tion to foliar venation patterns. The reductions in the degree of leaf vascularization of some needle-leaved *Hibbertia* species and of *Pachynema* are, in fact, specializations of a type not represented by Hickey's four evolutionary ranks of leaf venation. It is more accurate to refer to such "underdeveloped" leaf venation patterns as being morphological divergences rather than morphological regressions, since among reduced, xeromorphic leaves it is impossible to determine relative levels of specialization of venation (*sensu* Hickey, 1971b). The relative homogeneity of leaf venation patterns present in most genera of Dilleniaceae and the extreme heterogeneity of leaf venation of *Hibbertia* appear to be products resulting from adaptive radiation within different environments.

An evolutionary series of leaf and leaf venation types, based upon relative levels of vegetative morphological specialization observed within *Hibbertia* and other genera, is postulated for the entire family Dilleniaceae in CHART 1.

CHART 1. **Evolutionary trends of leaf venation patterns of Dilleniaceae.**

REDUCED LEAVES (L. S. 1, 2)	INTERMEDIATE-SIZED LEAVES (L. S. 2, 3)	"NORMAL"-SIZED LEAVES (L. S. 3, 4)

TYPE IA
TRILACUNAR &
UNILACUNAR
(*H. fasciculata*)

TYPE IB1
TRILACUNAR
(*H. glomerosa*) →

TYPE IB2
TRILACUNAR
(*H. amplexicaulis*)

↓

TYPE IB3
TRILACUNAR
(*H. dentata*)

?

↓ ↙   ↘ *

TYPE IIB   ?   TYPE IIB   TYPE IIIA
UNILACUNAR ←——————— TRILACUNAR   TRILACUNAR
(*H. nitida*)   (*H. virotii*)   (*H. serrata*)

↓   ↓   ↓

TYPE IIA2   TYPE IIIB
UNILACUNAR   TRILACUNAR
(*H. pungens*)   (*H. grossulariifolia*)

↓   ↓   ↓

TYPE IIA1   FOURTH RANK   FOURTH RANK
UNILACUNAR   BROCHIDODROMY   CRASPEDODROMY
(*H. acicularis*)   TRILACUNAR or   MULTILACUNAR
                     MULTILACUNAR   (*Dillenia*)
                     (*Tetracera*)

———————————————
* Occurs ontogenetically in several species of *Hibbertia*.
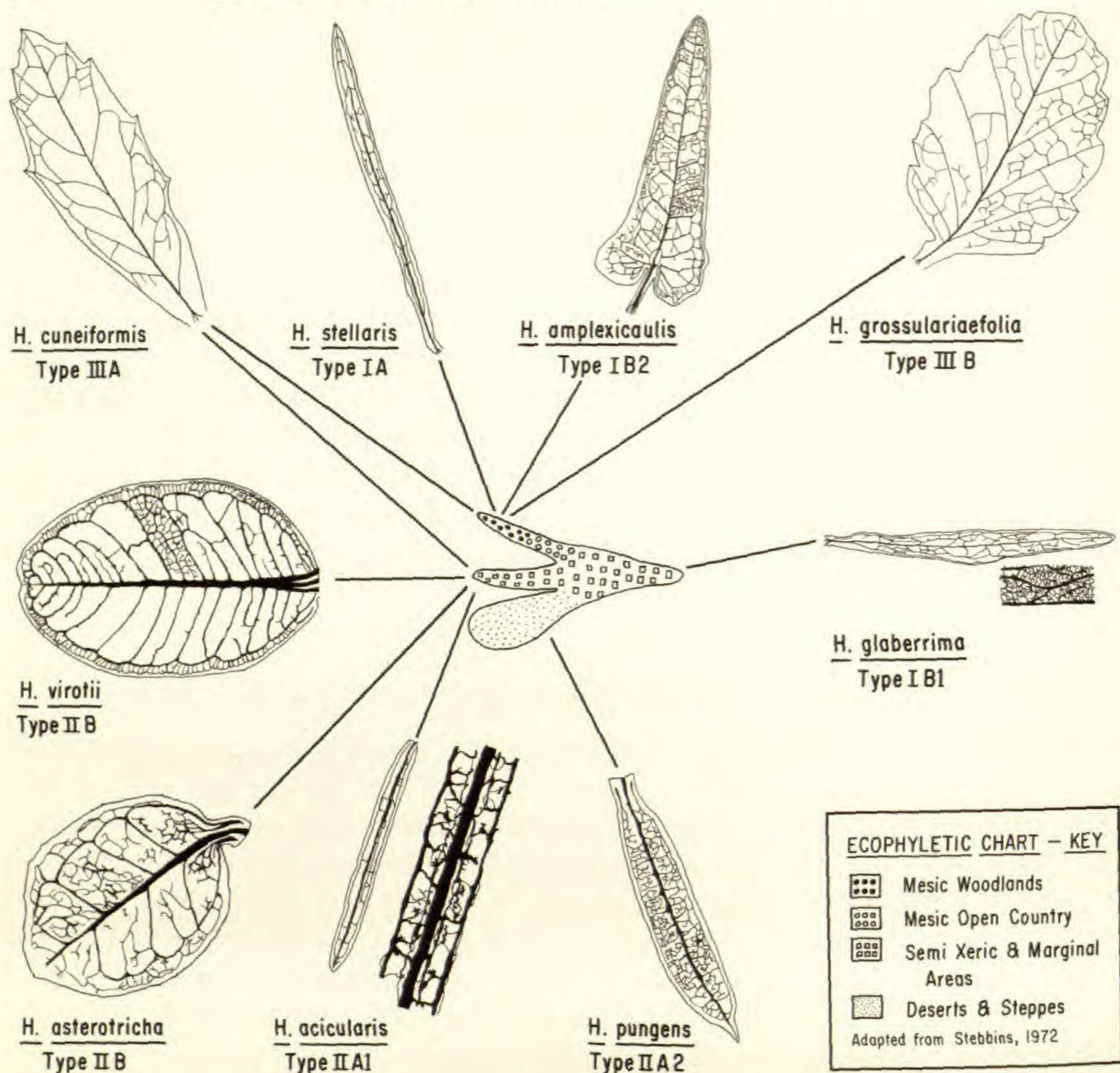
FIGURE 1. Adaptive radiation and leaf venation of *Hibbertia*. (Adapted from Stebbins with permission from the author and publisher.)

ADAPTIVE RADIATION WITHIN THE DILLENIACEAE.

Generalized habitat data, assembled for species of *Hibbertia* and for the other genera of Dilleniaceae, are employed in considerations of the structural diversification within *Hibbertia* and the entire family Dilleniaceae. Detailed information about their microhabitats and microclimatic preferences was not available. The morphological diversity of leaf venation patterns is illustrated in conjunction with the presumed patterns of adaptive radiation as envisioned by Stebbins (1972) for *Hibbertia* (FIGURE 1) and for the entire family (FIGURE 2).

Adaptive radiation, as defined by Radford *et al.* (1974, p. 543), is "evolutionary diversification within a group of related species or other taxa brought about by adaptations to different selective forces through time or migration." Stebbins (1974) has considered this phenomenon at some length and outlines several adaptations which generally occur in response to environmental conditions. Adaptations commonly selected for by drought or cold are: (1) reduction in growth, and therefore in size, of a plant;
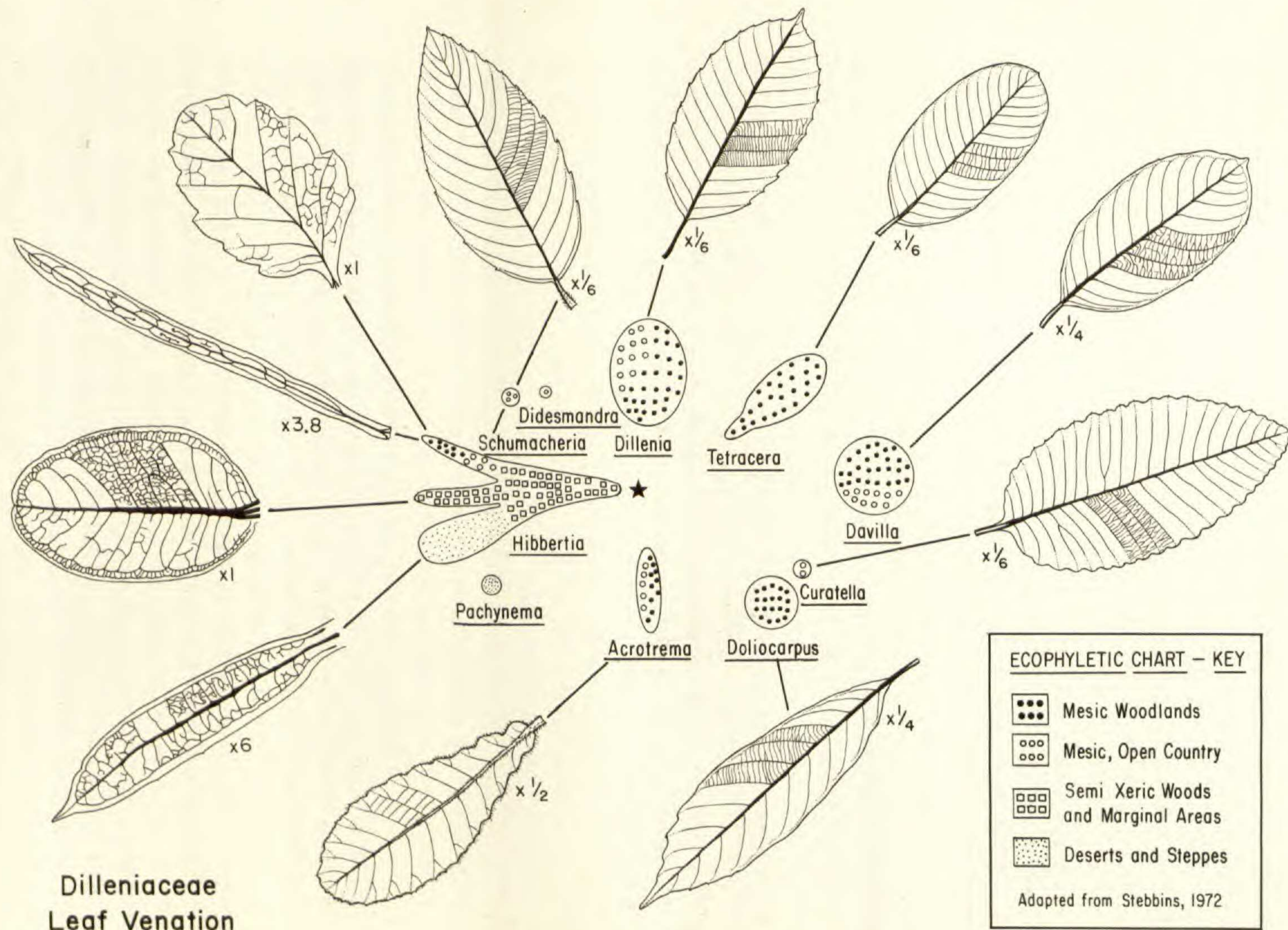
FIGURE 2. Adaptive radiation and leaf venation of Dilleniaceae. (Adapted from Stebbins with permission.)

(2) acquisition of physiological specializations; (3) hormonal adjustments to coordinate flowering with favorable seasons; and (4) reductions in growth that result in condensations of floral structure in response to the shortening of the favorable flowering-fruiting season. Conversely, Stebbins also outlined several changes that are fostered by an improving environment: (1) increased growth vigor and resultant increased plant size; (2) production of more and larger seeds; and (3) an increase in the number of potential animal pollinators.

Stebbins (*loc. cit.*) proposed a semi-xeric origin for the Dilleniaceae from which there was adaptive radiation into all habitats presently occupied by dilleniaceous taxa. The genus *Hibbertia*, which exhibits its greatest morphological diversity within such habitats (FIGURE 1), supports Stebbins's hypothesis concerning the original habitat of the Dilleniaceae. This correlation of extreme morphological diversity within semi-xeric habitats is also illustrated by the Dilleniaceae at the generic level. *Hibbertia* is both the most ecologically widespread and the most morphologically diverse genus of the family.

The reduced plant size of many hibbertias and all species of *Pachynema* is a response to the harsh, xeric habitats in which they occur. The reduced plant habit has also resulted in reduced leaf size in all xeric and numerous semi-xeric species of *Hibbertia*, as well as in the species of the xeric genus *Pachynema*. Reduced leaf size is an ecological adaptation which minimizes leaf surface area, thus retarding water loss and surface heating, enabling the plant to withstand prolonged drought seasons. The hibbertias and pachynemas of both semi-xeric and xeric habitats experience seasonal drought as do numerous other plants of the Australian "sclerophyll communities" (Specht, 1963). Leaf size reduction has been accompanied in *Pachynema* and numerous species of *Hibbertia* by the acquisition of other xeromorphic foliar features such as woolly vestiture, revolute margins, and stomatal crypts, all of which are extremely rare in the leaves of mesic species. Such reduced, xeromorphic leaves have been noted by Carlquist (1974) to be exceedingly common in plants of southwestern Australia, a region where numerous species of *Hibbertia* occur. Leaf venation patterns of xeric species commonly exhibit massive primary and intramarginal veins, massive intramarginal vein termini within the leaf base, and areolation that is lacking or poorly developed (see PLATES III, B, C; VI, C). The "regressions" in leaf venation organization exhibited by these hibbertias of extreme habitats are commonly observed in many woody dicotyledons growing in such environments (Hickey, 1971b). Reductions in overall leaf size have apparently resulted in a relatively massive primary vein as compared to leaf width. The similarity of leaf venation patterns among both small- and large-leaved *Hibbertia* species suggests that leaf size is a more variable character than is the pattern of leaf venation. The experimental induction of leaf expansion in various small-leaved Australian taxa, through the addition of phosphorous to pot cultures, also indicates that leaf size is a much more plastic, environmentally controlled character than is leaf venation (Beadle, 1968). It appears, therefore, that numerous

xerophytic species of *Hibbertia* have adapted "along the path of least resistance" (*sensu* Stebbins, 1974) through a reduction in leaf growth and expansion, rather than a rearrangement or reduction, of the leaf procambial network. Reductions in nodal anatomy from the generalized, trilacunar condition to the specialized, unilacunar condition have also occurred. Trilacunar, three-trace nodal patterns do not occur in xeric species of *Hibbertia*; conversely, unilacunar nodes are very rare in the mesic species. Numerous hibbertias and all species of *Pachynema* exhibit reductions in the number of perianth parts that are apparently a response to seasonal drought, an adaptation considered common for angiosperms in general (Stebbins, 1974).

Numerous morphological changes that commonly accompany plant radiation into more favorable habitats are illustrated by many species of *Hibbertia* and by all mesic genera of the Dilleniaceae. Morphological changes that have accompanied such a radiation are present in the mesic Australian species of *Hibbertia* and in the hibbertias that inhabit the more equable island habitats of New Caledonia, New Guinea, Fiji, and Madagascar. Increased plant size and vigor have resulted in the formation of large rosette trees of the New Caledonian hibbertias. Increased growth vigor is also evident in the mesic, lianoid taxa *Hibbertia scandens* and the genera *Davilla* and *Tetracera*. The arboreal growth habit of *Dillenia*, a mesic Old World genus, illustrates the favorable effect of mesic habitats upon plant growth. The mesomorphic condition of the foliage of all mesic dilleniaceous genera and of most mesic species of *Hibbertia* is also correlated with an adaptive radiation into more favorable mesic habitats. The largest leaved forms of *Hibbertia*, for example, occur as rosette trees in New Caledonia. These species (e.g., *H. baudouinii*) commonly inhabit moist montane regions of this equable island habitat and exhibit steady transpiration rates and vessel diameters comparable to those of mesic, woody dicots (Carlquist, 1975). Leaf mesomorphy is also striking in other mesic genera of Dilleniaceae (e.g., *Dillenia*, *Tetracera*) that possess large microphyllous or mesophyllous leaves. The differentiation of distinct petioles has also accompanied adaptive radiations into more mesic habitats. All petiolate species of *Hibbertia* (e.g., *H. banksii*, *H. coriacea*, *H. dentata*) and most petiolate genera of Dilleniaceae inhabit mesic regions and/or equable island habitats such as New Caledonia, New Guinea, or Madagascar, whereas petiolate leaves do not occur in xeric species. The more specialized petiolate condition, accordingly, appears to have arisen only within mesic habitats in dilleniaceous taxa. *Curatella*, however, a petiolate genus that inhabits open areas which are drier than areas inhabited by genera such as *Dillenia* and *Tetracera*, possesses pentalacunar nodes, well-developed petioles, and toothed leaves with fourth rank, simple craspedodromous venation. The presence of these vegetative specializations which are commonly restricted to mesic dilleniaceous taxa suggests that *Curatella* has experienced a secondary radiation from mesic habitats into more xeric, open areas. The absence of xeromorphic features, such as woolly vestiture and revolute leaf margins, is also evident in the leaves

of mesic genera and species of Dilleniaceae. Strong intramarginal veins, a specialization that presumably strengthens the leaf, occur in leaves of several species which inhabit islands with relatively equable climates (e.g., *H. coriacea* of Madagascar; all New Caledonian and Fijian species). The possession of "pre-teeth" (e.g., *H. cunninghamii*) and vascularized marginal teeth are features of leaf morphology generally restricted to mesic genera and species. Marginal teeth of the dillenioid type (Hickey & Wolfe, 1975), most common in the mesic species of *Hibbertia* and also in the genera *Curatella, Dillenia, Didesmandra,* and *Tetracera,* probably serve a hydathodal function.

The occurrence of reduced leaves in several mesic or hydric species of *Hibbertia* (e.g., *H. salicifolia, H. stellaris, H. stirlingii*) represents an exception to the general occurrence of microphylly and mesophylly in the mesic habitat. This may represent leaf-size reductions in response to an extreme, hydric habitat, or secondary migrations of xeromorphic species into a mesic-hydric habitat where their xeromorphic characters are not disadvantageous.

Increased specialization in leaf venation has also accompanied the adaptive radiation of numerous hibbertias and other dilleniaceous genera into more favorable habitats. The best-developed leaf venation of *Hibbertia,* for example, occurs in species from equable island habitats such as *H. banksii* from New Guinea, *H. coriacea* from Madagascar, and *H. lucens* from Fiji and New Caledonia. The contention of Hickey and Doyle (1972b) that evolutionary increase in the regularity of vein orders of woody dicot leaves has progressed from low order to high order veins is supported by the leaves of *H. grossulariifolia* and numerous New Caledonian species. These plants possess leaves with very regular low order (secondary) veins but exhibit much less regularity in their high order venation. Leaves of other mesic dilleniaceous genera, however, are quite specialized in their possession of very regular low and high order venation, a highly specialized system of rigidly percurrent tertiary venation, and a well-developed system of areoles (see PLATE XII). A system of percurrent tertiary veins has been interpreted to be an advanced feature of amentiferous leaves (Wolfe, 1973), and an advanced feature of highly specialized, "fourth rank" leaves of woody dicotyledons in general (Hickey, 1971b). The occurrence of terminal idioblasts in the leaves of many mesic hibbertias (e.g., *H. grossulariifolia, H. linearis*) is a striking contrast to the condition found by Sehgal and Paliwal (1974) in the leaves of *Euphorbia,* where idioblasts occur only in the xeric species. The significance of terminal idioblasts in the leaves of mesic hibbertias in unclear. Nodal anatomy has apparently undergone an amplification from the primitive trilacunar condition to an advanced multilacunar condition in all mesic genera of Dilleniaceae except *Hibbertia* and *Tetracera* (Dickison, 1969). A summary of the morphological features acquired by dilleniaceous taxa during their ancient adaptive radiations is presented in TABLE 2.

TABLE 2. Summary of morphological characteristics that have resulted from adaptive radiations within the family Dilleniaceae.

XERIC RADIANTS

1. Reductions in leaf size (*Hibbertia* and *Pachynema*).
2. Development of xeromorphic anatomical leaf features.
3. "Regression" in level of specialization of leaf venation patterns.
4. Development of a massive primary vein and massive intramarginal veins in the reduced leaves.
5. Reduction in nodal pattern to a unilacunar, one-trace condition with which massive, basal intramarginal vein termini are associated.
6. Decrease in plant size and growth vigor.
7. Overall reductions in floral morphology and anatomy, including reduced seed production per flower.

MESIC RADIANTS

1. Development of larger leaves (L. S. 3, 4) with well-developed petioles with three or more fused leaf traces.
2. Development (in numerous cases) of marginal, dillenioid teeth and very regular, simple craspedodromous venation in the leaves.
3. Development of a rigidly percurrent tertiary vein system enclosing a system of well-developed areolation in the leaves.
4. Amplification of trilacunar nodes to a multilacunar condition in mesic genera other than *Hibbertia* and *Tetracera*.
5. Increase in plant size and growth vigor.
6. Reduction in carpel number and number of ovules per carpel.
7. Increase in carpel and/or ovule number in several cases.
8. Amplification of stamen number, presumably in response to coleopteran pollination.
9. Development of various degrees of basal or lateral syncarpy.

CONCLUSIONS

1. The extreme diversity of leaf morphology and venation patterns of *Hibbertia* has resulted from radiation into and evolution within a wide range of ecological situations.
2. Numerous species of *Hibbertia* exhibit ontogenetic changes in leaf morphology and basic venation pattern. These changes, however, do not alter the high order vein configuration from the original juvenile condition.
3. The greatest diversity of leaf morphology and venation occurs within the Australian hibbertias.
4. New Caledonian hibbertias, which exhibit remarkably similar venation patterns, appear to be more variable in their floral structure than in their leaf morphology and venation.
5. The subgeneric sections of *Hibbertia* (*sensu* Gilg & Werdermann, 1925) generally constitute natural species assemblages on the basis of leaf morphology.
6. Several levels of evolutionary advancement in the organization of leaf venation are evident in species of *Hibbertia*.

7. Leaf venation patterns of some species of *Hibbertia* are the most unspecialized of the entire family Dilleniaceae.
8. Evolutionary trends in leaf morphology and venation, observed within *Hibbertia* and other genera of Dilleniaceae, are generally correlated with evolutionary trends observed elsewhere in the plant body.
9. Features of leaf morphology and venation of *Hibbertia* reveal vegetative character syndromes that are correlated with habitat.
10. Regressions in the level of organization of leaf venation below that characteristic of the genus are evident in the leaves of numerous hibbertias of extreme xeric or hydric habitats.
11. The best-developed leaf venation patterns generally occur in hibbertias of equable island habitats such as Fiji, Madagascar, New Caledonia, and New Guinea.
12. Ecophyletic specializations observed within species of *Hibbertia* closely parallel those observed, at the generic level, within the Dilleniaceae as a whole.

ACKNOWLEDGMENTS

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APPENDIX 1. Intrageneric treatment of Hibbertia Andrews
(sensu Gilg and Werdermann, 1925).

Section TRISEMA (Hooker) Gilg (ca. 10 species). New Caledonia. Inflorescence spicate. Sepals 5; petals 3 or 4; stamens numerous (50 to 100), encircling the single, terminal carpel; staminodia absent; carpel glabrous with 8 to 12 ovules. Species studied: *H. deplancheana* Bur. ex Guillaumin, *H. lucida* Bur. ex Guillaumin, *H. oubatchensis* Schltr., *H. pancheri* (Brongn. & Gris) Briq., *H. patula* Guillaumin, *H. vanieri* Beauvis., *H. wagapii* Gilg.

Section POLYSTICHE Baker (ca. 2 species). New Caledonia. Inflorescence spicate. Sepals 5; petals 5; stamens numerous (100+) encircling 3 or 4 carpels; staminodia absent; carpels glabrous with 15 or more ovules. Species studied: *H. baudouinii* Brongn. & Gris.

Section SPICATAE Baker (ca. 10 species). New Caledonia, Fiji. Inflorescence a secund spike. Sepals 5; petals 5; stamens numerous (65 to 100), encircling a pair of carpels; staminodia absent; carpels glabrous with 10 ovules each. Species studied: *H. altigena* Schltr., *H. brongniartii* Gilg, *H. lucens* Brongn. & Gris ex Seb. & Pancher, *H. ngoyensis* Schltr., *H. podocarpifolia* Schltr., *H. scabra* Brongn. & Gris, *H. trachyphylla* Schltr., *H. virotii* Guillaumin.

Section CYCLANDRA F. Mueller ex Gilg (ca. 50 species). Australia and New Caledonia. Floral structure is highly variable. Flowers pentamerous with numerous stamens surrounding the carpels on all sides.

Subsection FASCICULATAE Bentham (ca. 2 species). New South Wales, South Australia, Tasmania, and Victoria. Flowers sessile. Sepals 5; petals 5; stamens fasciculate, up to 20 in number; staminodia absent; carpels glabrous, 3 to 5, with 6 to 8 ovules each. Species studied: *H. fasciculata* R. Br. ex DC., *H. procumbens* (Labill.) DC.

Subsection BRACTEATAE Bentham (ca. 6 species). New South Wales, southwestern Australia, Tasmania, and Victoria. Flowers sessile. Sepals 5; petals 5; stamens 10 to 20 or 30 to 60; staminodia absent; carpels glabrous, 3 or 5, with 1 or 2 ovules each. Species studied: *H. miniata* Gardner, *H. montana* Steudel, *H. montana* var. *major* Steudel, *H. pilosa* Steudel, *H. serrata* Hotchkiss, *H. virgata* R. Br. ex DC.

Subsection SUBSESSILES Bentham (ca. 7 species). East Australia, southeast Australia, New South Wales, Queensland, and Victoria. Flowers sessile-terminal or axillary. Sepals 5; petals 5; stamens 15 to 30; staminodia absent; carpels 3, glabrous, with 1 or 2 ovules each. Species studied: *H. diffusa* R. Br. ex DC., *H. elata* Maiden & Betche, *H. linearis* R. Br. ex DC., *H. linearis* var. *obtusifolia* DC., *H. saligna* R. Br. ex DC., *H. scandens* (Willd.) Gilg, *H. scandens* var. *oxyphyllum* Domin.

Subsection BRACHYANTHERAE Bentham (ca. 3 species). Southwest Australia. Flowers pedunculate. Sepals 5; petals 5; stamens 11 to 20; staminodia absent; carpels glabrous, 3 or 5; with 1 or 2 ovules each. Species studied: *H. pungens* Bentham, *H. stellaris* Endl.

Subsection VESTITAE Bentham (ca. 3 species). East and southeast Australia. Flowers sessile or pedunculate. Sepals 5; petals 5; stamens 15 to 30 or more; staminodia present or absent; carpels 3, villous, with 4 to 6 ovules

each. Species studied: *H. pedunculata* R. Br. ex DC., *H. vestita* A. Cunn. ex Bentham.

Subsection TOMENTOSAE Bentham (ca. 10 species). North Australia, northeast Australia, east Australia, and southeast Australia. Flowers axillary-pedunculate. Sepals 5; petals 5; stamens 6 to 50 or more; staminodia few or absent; carpels 2, tomentose, with 1 to 3 ovules each. Species studied: *H. cistifolia* R. Br., *H. hermanniifolia* DC., *H. hexandra* C. T. White, *H. melhanoides* F. Mueller, *H. oblongata* R. Br. ex DC., *H. stirlingii* C. T. White, *H. tomentosa* R. Br.

Subsection HEMIHIBBERTIAE Bentham (ca. 14 species). Central Australia, east Australia, northwest Australia, and southwest Australia. Flowers pedunculate. Sepals 5; petals 5; stamens 20 to 200; staminodia present; carpels glabrous (except *H. grossulariifolia* and *H. lasiopus*), 3, 5, or 8 to 15, with 2 to 8 ovules each. Species studied: *H. amplexicaulis* Steudel, *H. cunninghamii* Hooker, *H. dentata* R. Br. ex DC., *H. gilgiana* Diels, *H. glaberrima* F. Mueller, *H. grossulariifolia* (Salisb.) Salisb., *H. lasiopus* Bentham, *H. longifolia* F. Mueller, *H. mylnei* Bentham, *H. nymphaea* Diels, *H. perfoliata* Endl., *H. potentilliflora* F. Mueller ex Bentham, *H. quadricolor* Domin.

Subsection TRIMORPHANDRA (Brongn. & Gris) Baker (ca. 2 species). New Caledonia. Inflorescence spicate or flowers solitary, sessile. Sepals 5, petals 5, stamens numerous; staminodia present; carpels 2, glabrous, with 3 to 5 ovules. Species studied: *H. heterotricha* Bur. ex Guillaumin, *H. pulchella* (Brongn. & Gris) Schltr.

Subsection SALICIFOLIAE Gilg (one species). East Australia. Flowers axillary-sessile. Sepals 5; petals 5; stamens 10, filaments forming a tube; staminodia absent; carpels 2, glabrous and uniovulate. Species studied: *H. salicifolia* F. Mueller.

Section CANDOLLEA (Labill.) F. Mueller (ca. 12 species). Southwest Australia. Sepals 5; petals 5; stamens 10 to 35 in 5 bundles of 2 to 7 stamens each; staminodia absent; carpels 3 or 5, glabrous, with 1 to 3 ovules each.

Subsection SESSILES Gilg (ca. 8 species). Flowers axillary-sessile. Species studied: *H. cuneiformis* (Labill.) Sm., *H. enervia* (DC.) Hoogl., *H. glomerosa* (Bentham) F. Mueller, *H. huegelii* (Endl.) F. Mueller, *H. pachyrrhiza* Steudel, *H. tetrandra* (Lindley) Gilg.

Subsection PEDUNCULATAE Gilg (ca. 4 species). Flowers axillary-pedunculate. Species studied: *H. racemosa* (Endl.) Gilg, *H. subvaginata* (Steudel) F. Mueller, *H. uncinata* (Bentham) F. Mueller.

Section HEMIPLEURANDRA Bentham. Southwest Australia.

Subsection UNIFLORAE Gilg (ca. 10 species). Flowers axillary-pedunculate. Sepals 5; petals 5; stamens declinate (on one side of gynoecium), rarely more than 12; staminodia present; carpels 2, villous, with 2 to 4 ovules each. Species studied: *H. aurea* Steudel, *H. furfuracea* (R. Br. ex DC.) Bentham, *H. hypericoides* (DC.) Bentham, *H. microphylla* Steudel, *H. rhadinopoda* F. Mueller, *H. silvestris* Diels.

Section HEMISTEMMA (Juss.) Bentham (ca. 8 species). Inflorescence spicate with two or more flowers. Sepals 5; petals 5; stamens numerous (up to 50),

declinate; staminodia numerous (up to 60); declinate; carpels 2, villous, with 2 or 3 ovules each.

Subsection OPPOSITIFOLIAE Gilg (one species). Madagascar. Opposite leaf arrangement. Species studied: *H. coriacea* (Pers.) Baillon.

Subsection ALTERNIFOLIAE Gilg (ca. 7 species). New Guinea, northern Australia. Alternate leaf arrangement. Species studied: *H. angustifolia* (R. Br. ex DC.) Bentham, *H. banksii* (R. Br. ex DC.) Bentham, *H. dealbata* (R. Br. ex DC.) Bentham, *H. holtzei* F. Mueller, *Hibbertia* sp. 1.

Section PLEURANDRA (Labill.) Bentham (ca. 13 species). East Australia, southeast Australia, and Western Australia. Flowers sessile, solitary-pedunculate, or in solitary heads. Sepals 5; petals 5; stamens declinate and few, rarely more than 15; staminodia absent; carpels 2, generally villous or tomentose, with 2 to 4 ovules each.

Subsection PLATYPHYLLAE Gilg (ca. 8 species). Leaves generally small, flat, and broad. Species studied: *H. aspera* DC., *H. asterotricha* (Sieber ex Sprengel) N. A. Wakefield, *H. bracteata* (R. Br. ex DC.) Bentham, *H. cistiflora* N. A. Wakefield, *H. cistoidea* (Hooker) C. T. White, *H. nitida* (R. Br. ex DC.) F. Mueller, *H. sericea* (R. Br. ex DC.) Bentham, *H. stricta* (DC.) F. Mueller.

Subsection ACICULARES Gilg (ca. 5 species). Leaves linear and needle-like. Species studied: *H. acicularis* (Labill.) F. Mueller, *H. exutiacies* N. A. Wakefield, *H. gracilipes* Bentham, *H. mucronata* Bentham.

Section uncertain (ca. 40 species) (presently being revised by Prof. R. D. Hoogland, The Australian National University). New Caledonia and Australia. Species studied: *H. ebracteata* Bur. ex Guillaumin, *H. inconspicua* Ostf., *H. nana* Däniker, *H. tontoutensis* Guillaumin, *Hibbertia* sp. 2, *Hibbertia* sp. 3.

EXPLANATION OF PLATES

PLATE I

Leaf venation of *Hibbertia*, section TRISEMA. Scale indications represent 1 mm. A, *H. lucida* (*Baumann-Bodenheim 15829*). B, *H. oubatchensis* (*H. S. McKee 3371*). C, D, *H. deplancheana* (*R. F. Thorne 28232*).

PLATE II

Leaf venation of *Hibbertia*, sections POLYSTICHE (A) and SPICATAE (B–D). Scale indications represent 1 mm. A, *H. baudouinii* (*J. T. Buchholz 1577*). B, *H. virotii* (*R. Virot 161*). C, *H. altigena* (*H. S. McKee 3709*). D, *H. ngoyensis* (*Guillaumin & Baumann-Bodenheim 12555*).

PLATE III

Leaf venation of *Hibbertia*, section CYCLANDRA, subsections SUBSESSILES (F–I), BRACHYANTHERAE (A–C), VESTITAE (D, E). Scale indications represent 1 mm. A, *H. stellaris* (*A. M. Ashby 2007*). B, C, *H. pungens* (*Royce 7640*).

D, *H. pedunculata* (*Anon. s.n.*, A). E, *H. vestita* (*E. F. Constable 6382*). F–H, *H. linearis* (*C. T. White 8580*). I, *H. scandens* var. *oxyphyllum* (*NCU 423743*).

PLATE IV

Leaf venation of *Hibbertia*, section CYCLANDRA, subsection HEMIHIBBERTIAE. Scale indications represent 1 mm. A, *H. glaberrima* (*D. J. Whibley 1081*). B, *H. gilgiana* (*C. L. Wilson 856*). C, *H. dentata* (*Cult. s.n.*, K). D, *H. amplexicaulis* (*E. Pritzel 531*). E, F, *H. grossulariifolia* (*C. L. Wilson 851*). G, *H. nymphaea* (*A. Morrison s.n.*).

PLATE V

Leaf venation of *Hibbertia*, section CYCLANDRA, subsections TOMENTOSAE (A, C–F), TRIMORPHANDRA (G–I), and SALICIFOLIAE (B). Scale indications represent 1 mm. A, *H. cistifolia* (*R. L. Specht 843*). B, *H. salicifolia* (*C. L. Wilson 625*). C, *H. tomentosa* (*R. L. Specht 638*). D, E, *H. stirlingii* (*C. L. Wilson 757*). F, *H. hexandra* (*E. F. Constable 1362*). G–I, *H. pulchella* (*Franc 1597*).

PLATE VI

Leaf venation of *Hibbertia*, sections CANDOLLEA (A–C, G, I–K) and HEMIPLEURANDRA (D–F, H, L–N). Scale indications represent 1 mm. A, *H. cuneiformis* (*E. H. Wilson 297*). B, *H. pachyrrhiza* (*C. L. Wilson 861*). C, *H. uncinata* (*C. L. Wilson 155*). D, E, *H. hypericoides* (*M. H. Jones 34*). F, *H. rhadinopoda* (*E. Pritzel 97*). G, *H. racemosa* (*C. L. Wilson 811*). H, *H. microphylla* (*C. T. White 5317*). I, *H. huegelii* (*C. L. Wilson 777*). J, *H. tetrandra* (*E C3544*). K, *H. subvaginata* (*C. L. Wilson 764*). L, M, *H. aurea* (*C. L. Wilson 843*). N, *H. furfuracea* (*C. T. White 5382*).

PLATE VII

Leaf venation of *Hibbertia*, section HEMISTEMMA. Scale indications represent 1 mm. A, *H. angustifolia* (*Philson & Earle 111*). B, *H. banksii* (*L. J. Brass 8431*). C, *H. coriacea* (*H. Humbert 5866*). D, *H. banksii* (*L. J. Brass 19425*).

PLATE VIII

Leaf venation of *Hibbertia*, section PLEURANDRA. Scale indications represent 1 mm. A, *H. asterotricha* (*NCU 445391*). B, C, *H. acicularis* (*NCU 445396*). D, *H. stricta* (*T. B. Muir 2623*). E, *H. nitida* (*Fl. Novae Holl. 141*). F, *H. gracilipes* (*Royce 5792*). G, H, *H. sericea* (*E. F. Constable 3850*). I, *H. aspera* (*E. F. Constable 4311*). J, *H. mucronata* (*C. L. Wilson 792*).

PLATE IX

Leaf venation of *Hibbertia*, sections CYCLANDRA (C, F), PLEURANDRA (B, E), and uncertain (A, D, G). Scale indications represent 1 mm. A, *H. ebracteata* (*Guillaumin & Baumann-Bodenheim 11659*). B, *H. cistoidea* (*E. F. Constable 5139*). C, *H. tetrandra* (*C. L. Wilson 848*). D, G, *H. tontoutensis* (*McMillan 5060*). E, *H. cistiflora* (*S. Helms 1290*). F, *H. elata* (*R. Coveny 3737*).

PLATE X

Leaf venation of *Hibbertia*, sections CYCLANDRA (subsect. TOMENTOSAE) (A, B, E), HEMISTEMMA (D, F), and PLEURANDRA (C). A, *H. cistifolia* (*R. L. Specht 843*), × 2.4. B, *H. oblongata* (*R. L. Specht 427*), × 2.4. C, *H. bracteata* (*Anderson & Boorman s.n.*), × 2.3. D, *H. coriacea* (*H. Humbert 5866*), × 2. E, *H. melhanoides* (*C. L. Wilson 740*), × 2.3. F, *H. dealbata* (*R. L. Specht 844*), × 1.9.

PLATE XI

Leaf venation of *Hibbertia*, sections CYCLANDRA (A, C) and HEMISTEMMA (B). A, *H. linearis* var. *obtusifolia* (*Lazarides & Story s.n.*), × 2.3. B, *H. holtzei* (*US 2378199*), × 1.3. C, *H. cunninghamii* (*R. D. Royce 5774*), × 1.8.

PLATE XII

Leaf venation of Dilleniaceae. A, *Curatella americana* (*Irwin 5470*), × 2. B, *Hibbertia wagapii* (*R. F. Thorne 28266*), × 2. C, *Tetracera macrophylla* (*Cult. s.n.*, SING), × 1.7. D, *Doliocarpus major* (*MO 1245995*), × 1.8. E, *Dillenia albiflos* (*Anon. s.n.*), × 1.2. F, *Hibbertia trachyphylla* (*C. T. White 2126*), × 3. G, *Hibbertia lucens* (*A. C. Smith 1877*), × 2. H, *Hibbertia pancheri* (*Franc 2257*), × 2.

PLATE XIII

Details of leaf venation in *Hibbertia*. A, *H. aurea* (*C. L. Wilson 843*), node showing a single leaf trace, × 67. B, *H. uncinata* (*C. L. Wilson 155*), leaf base with single trace and lateral, massive intramarginal vein termini, × 63. C, *H. diffusa* (*E. F. Constable s.n.*), leaf base with three unfused traces × 50. D, *H. coriacea* (*H. Humbert 5866*), marginal ultimate leaf venation, × 67. E, *H. heterotricha* (*H. S. McKee 7753*), marginal ultimate leaf venation, × 67. F, *H. huegelii* (*C. L. Wilson 777*), intercostal leaf venation with free vein termini and idioblasts, × 67.

PLATE XIV

Marginal teeth of leaves of *Hibbertia*, exhibiting the dillenioid tooth structure. A, *H. cuneiformis* (*R. D. Hoogland 12536*), × 24. B, *H. grossulariifolia* (*C. L. Wilson 851*), × 76. C, *H. cuneiformis* (*Cult. s.n.*, K), × 101. D, *H. cunninghamii* (*R. D. Royce 5774*), "pretooth" of marginal ultimate venation, × 84. E, *H. linearis* var. *obtusifolia* (*Lazarides & Story s.n.*), × 168. (Photograph A courtesy of G. Ledyard Stebbins.)

PLATE XV

Details of *Hibbertia* leaf venation. A, *H. racemosa* (*C. L. Wilson 811*), note massive tracheary accumulations associated with apical-lateral teeth, × 91. B, *H. glomerosa* (*G. L. Stebbins A-5*), note irregularity of veinlets, × 16. C, *Hibbertia* sp. 1 (*Lazarides 7859*), × 2.4. D, *H. montana* (*R. D. Hoogland 12512*), note ramified intercostal veins, × 24. (Photographs B–D courtesy of G. Ledyard Stebbins.)

PLATE I

RURY & DICKISON, LEAF VENATION PATTERNS

PLATE II

RURY & DICKISON, LEAF VENATION PATTERNS

PLATE III

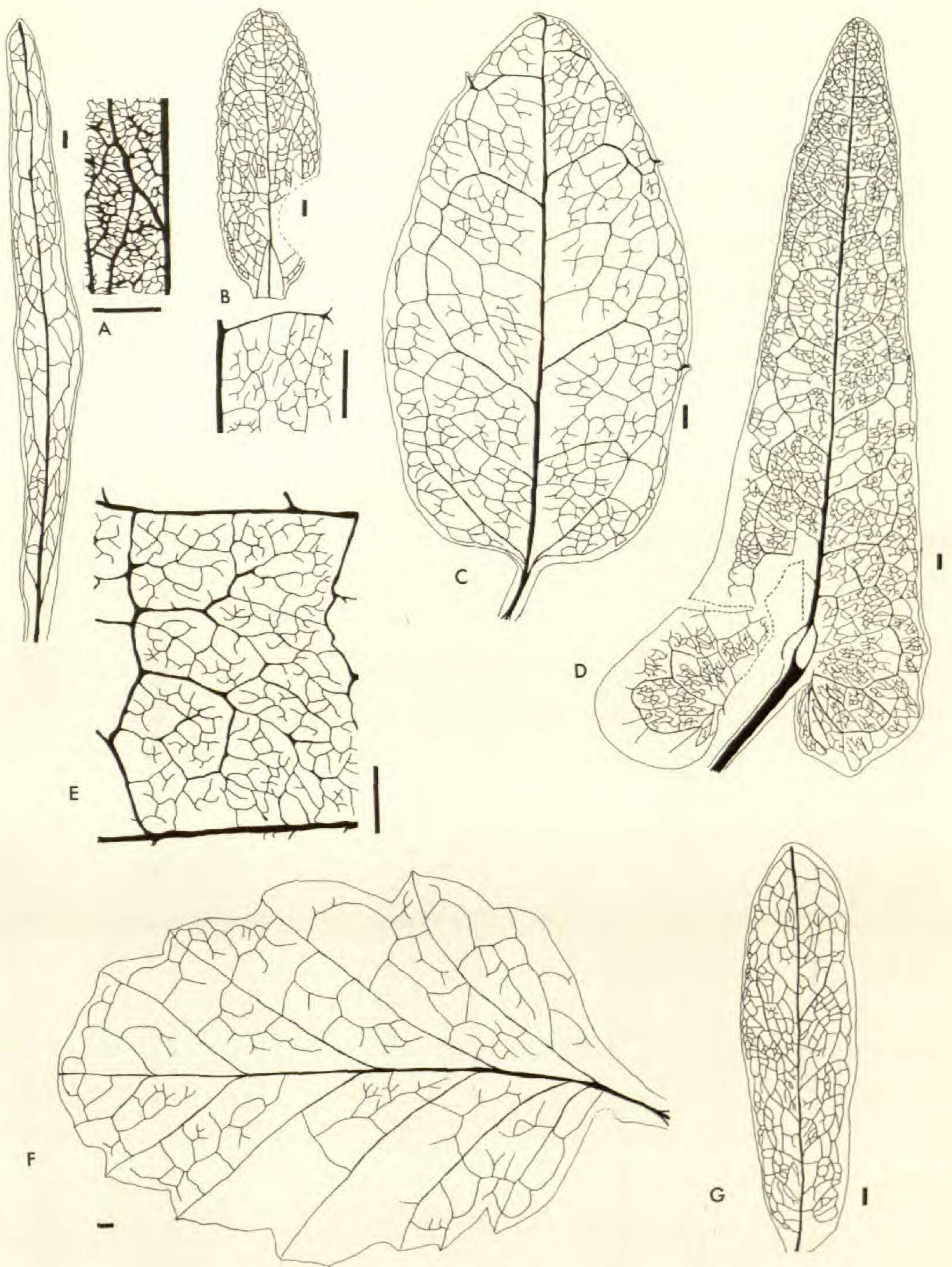RURY & DICKISON, LEAF VENATION PATTERNS

Plate IV

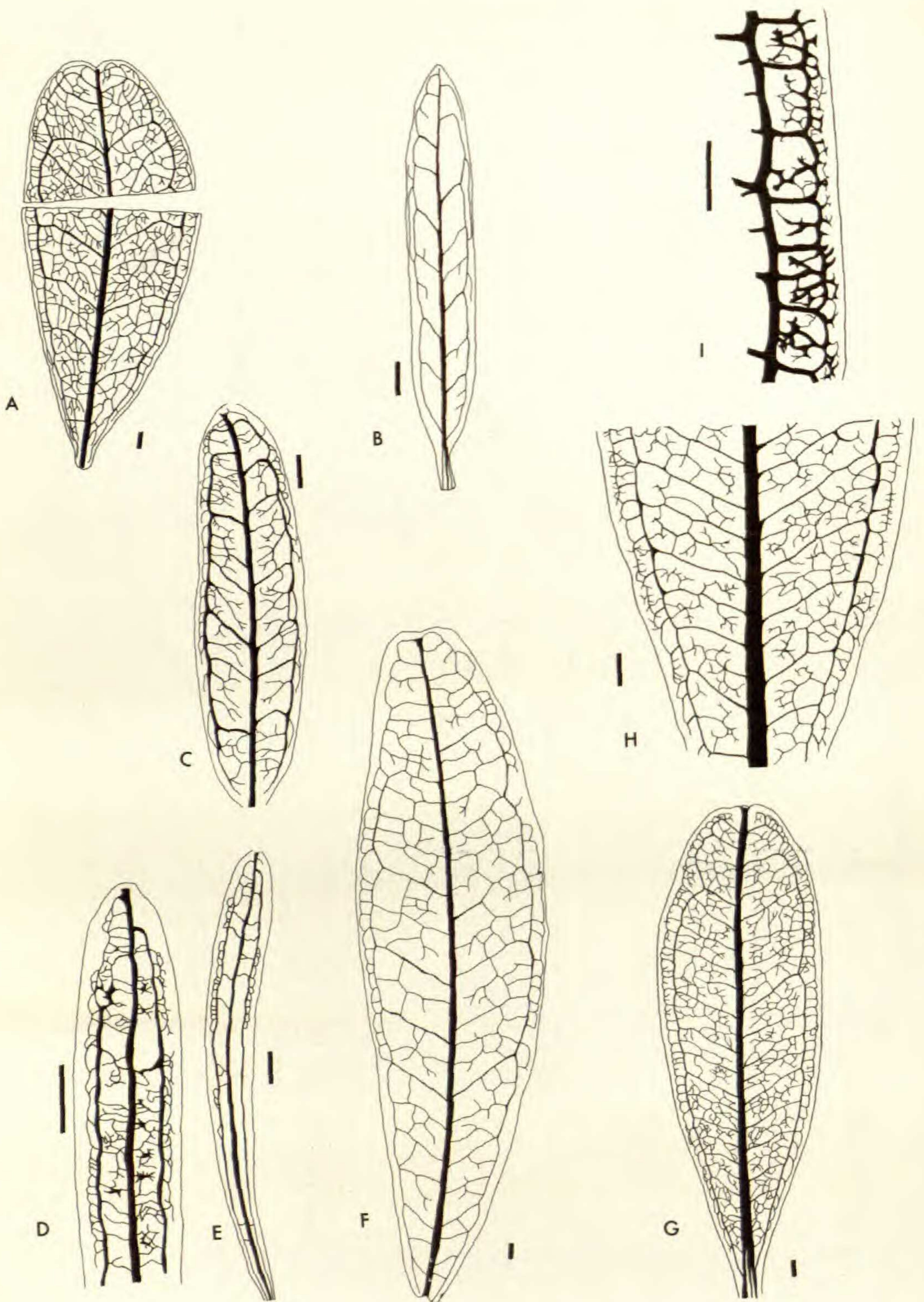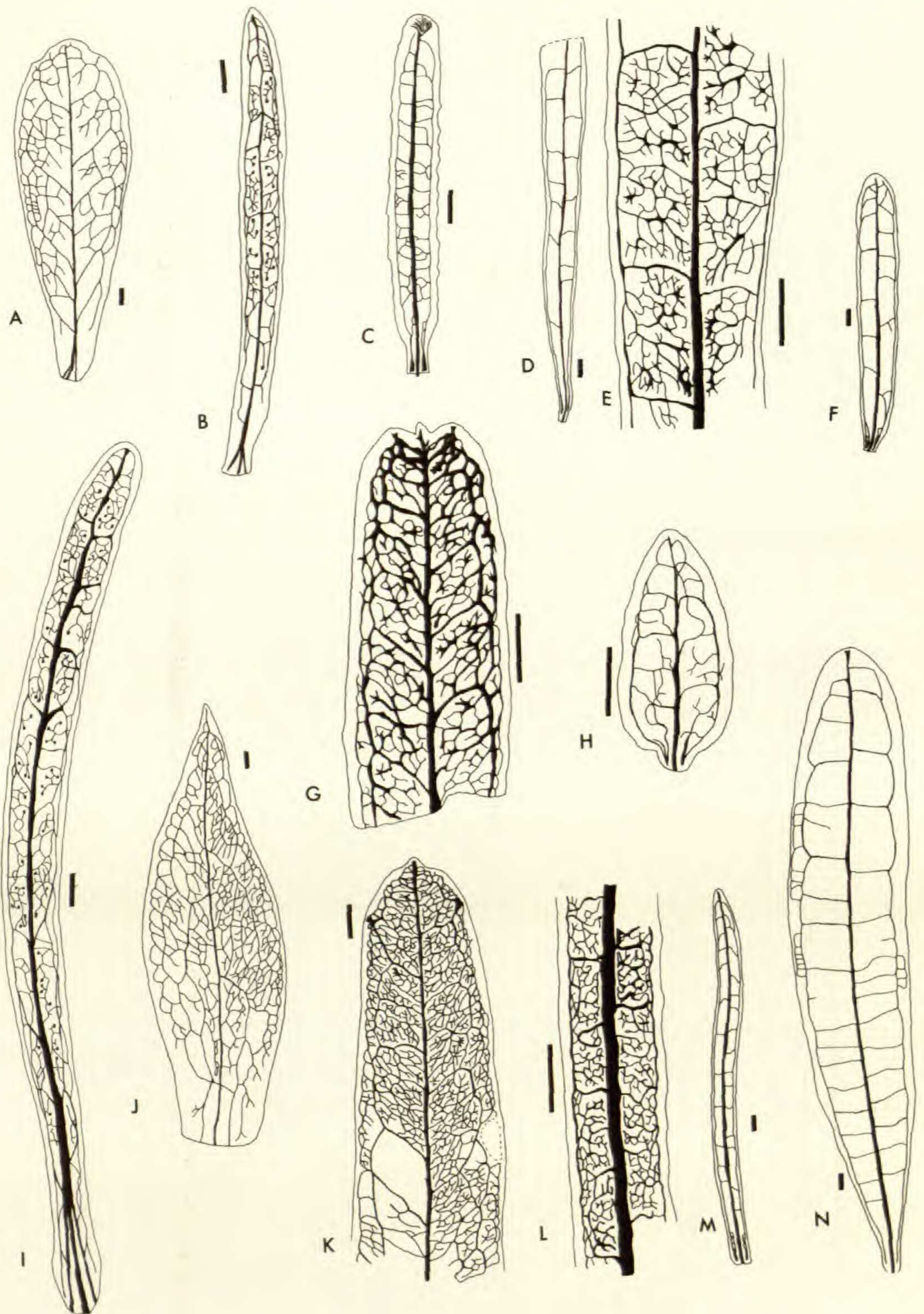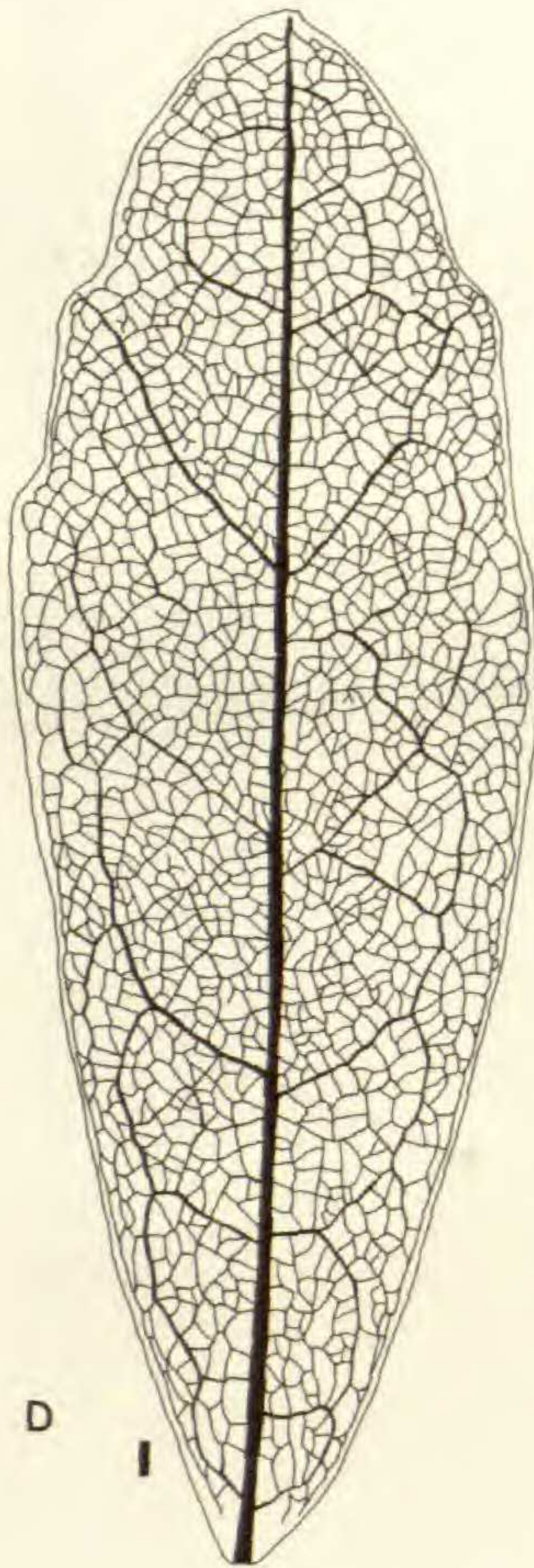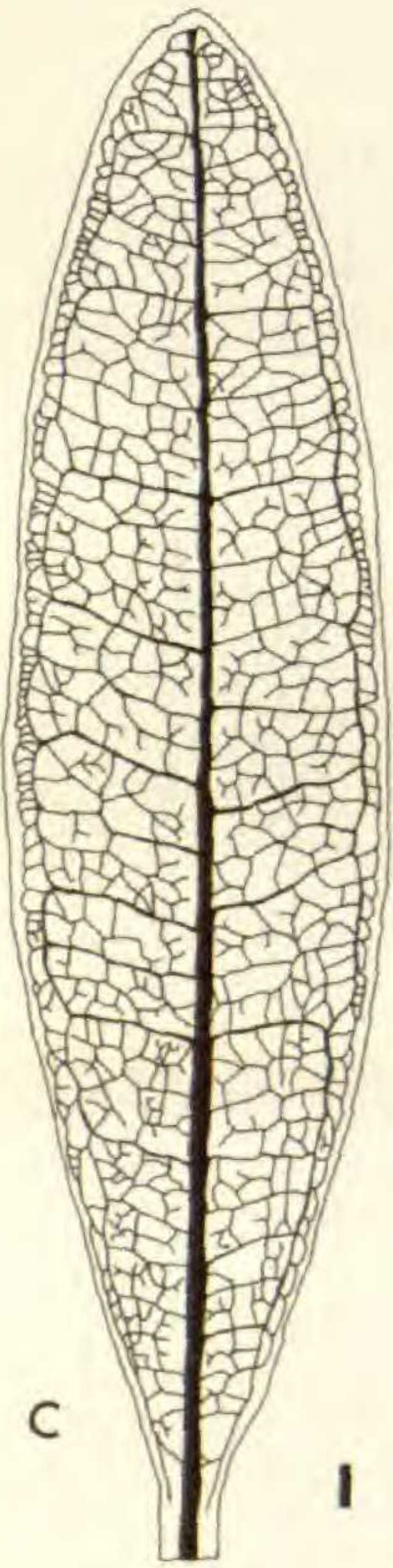RURY & DICKISON, LEAF VENATION PATTERNS

PLATE V

RURY & DICKISON, LEAF VENATION PATTERNS
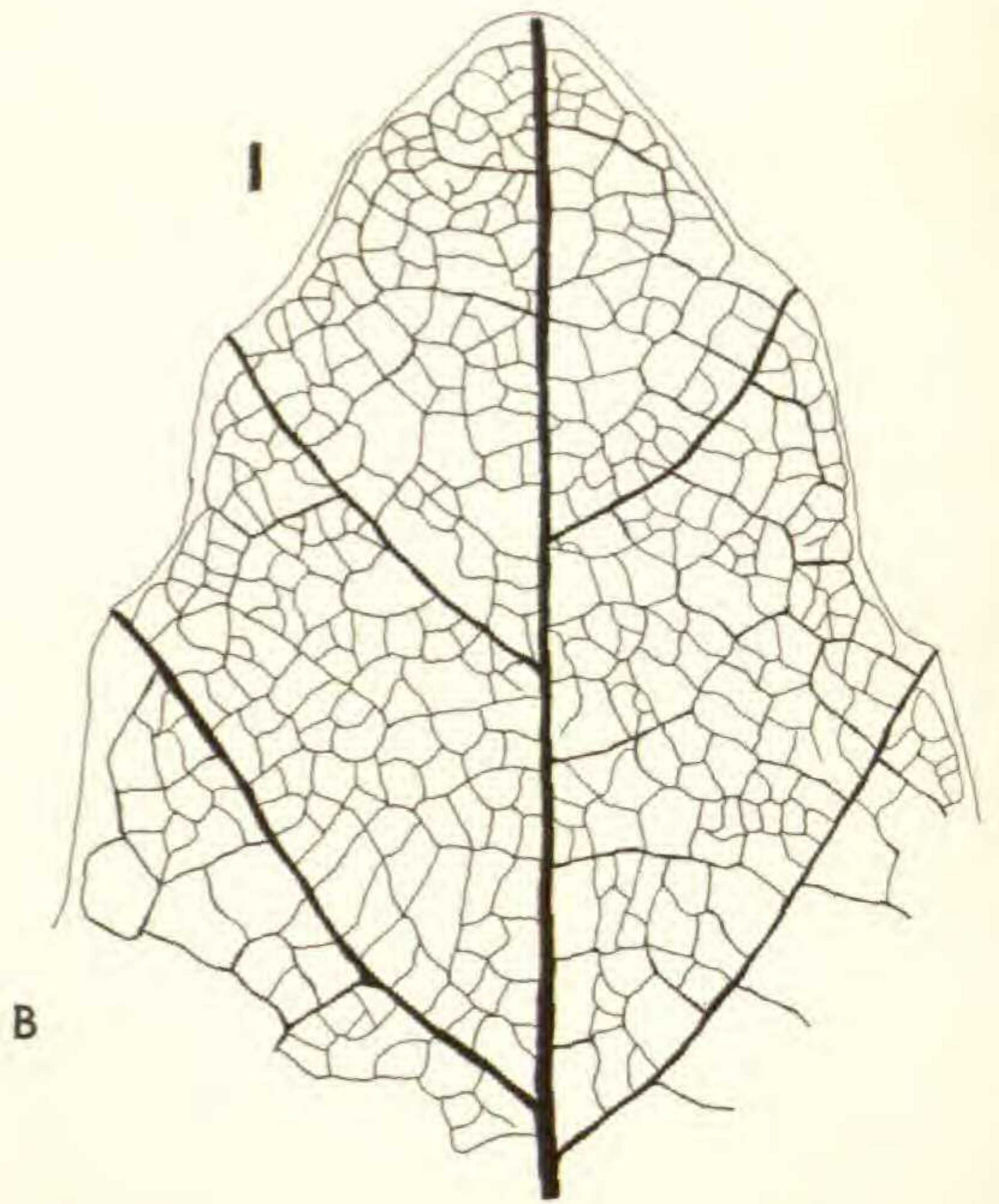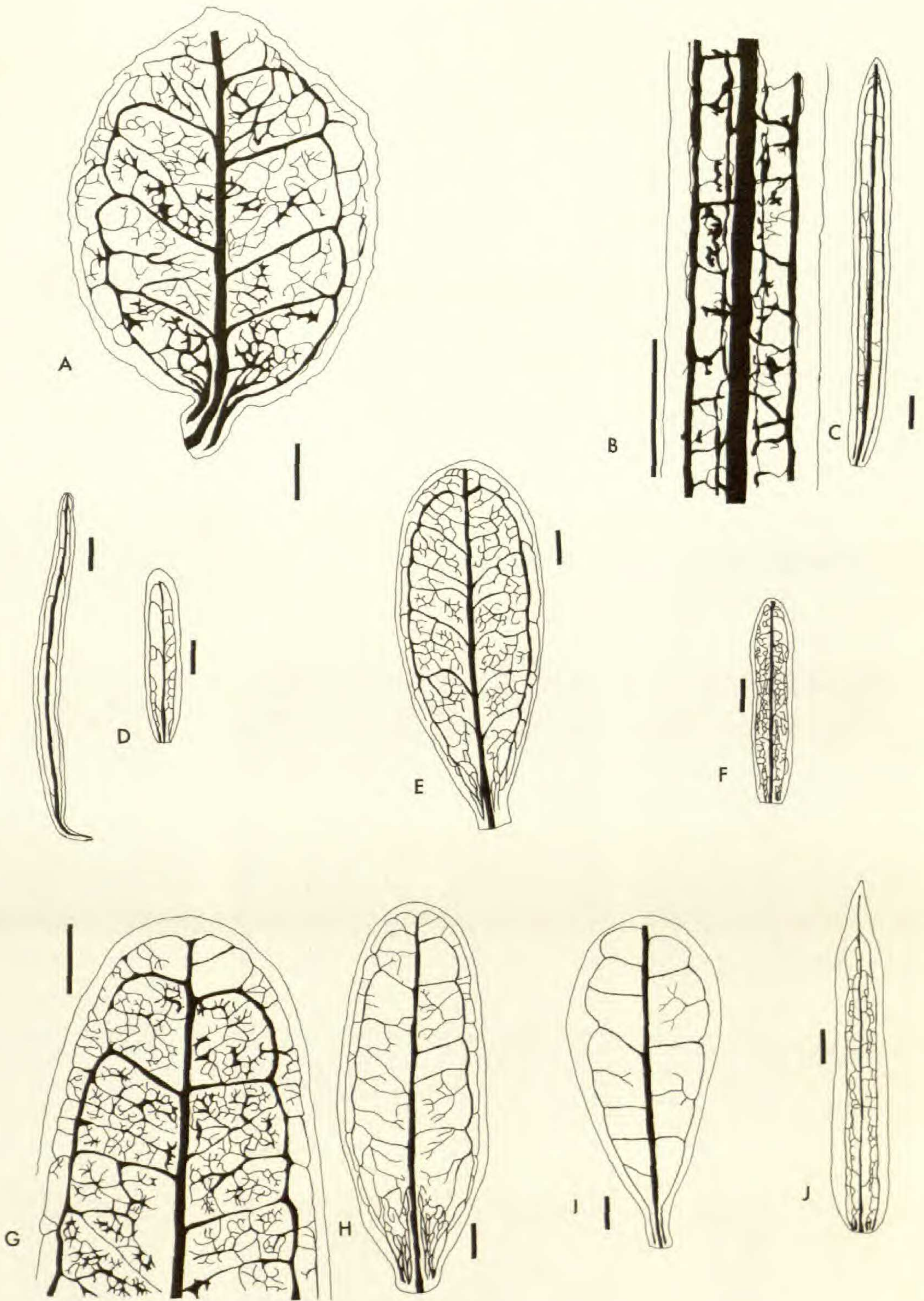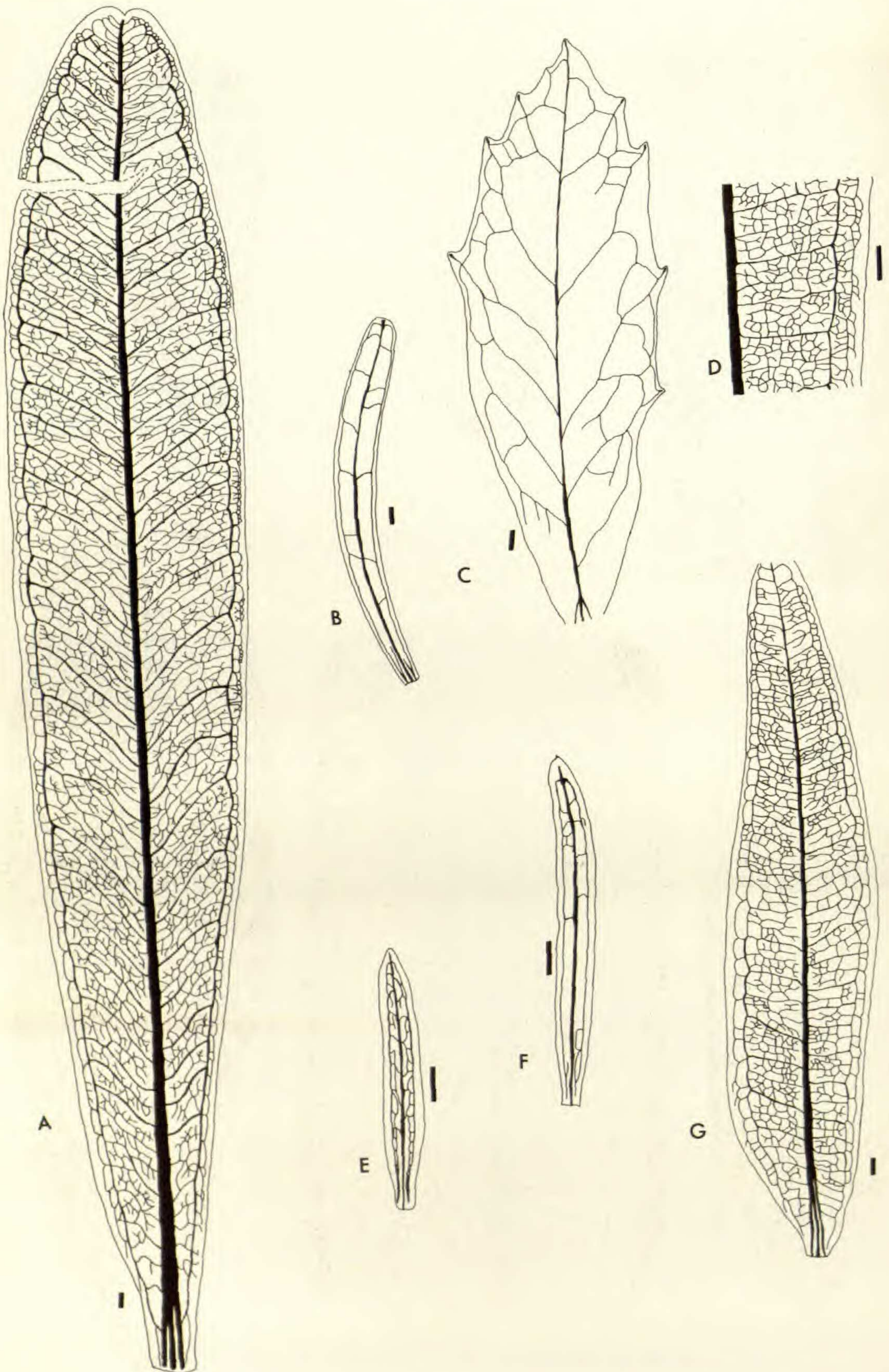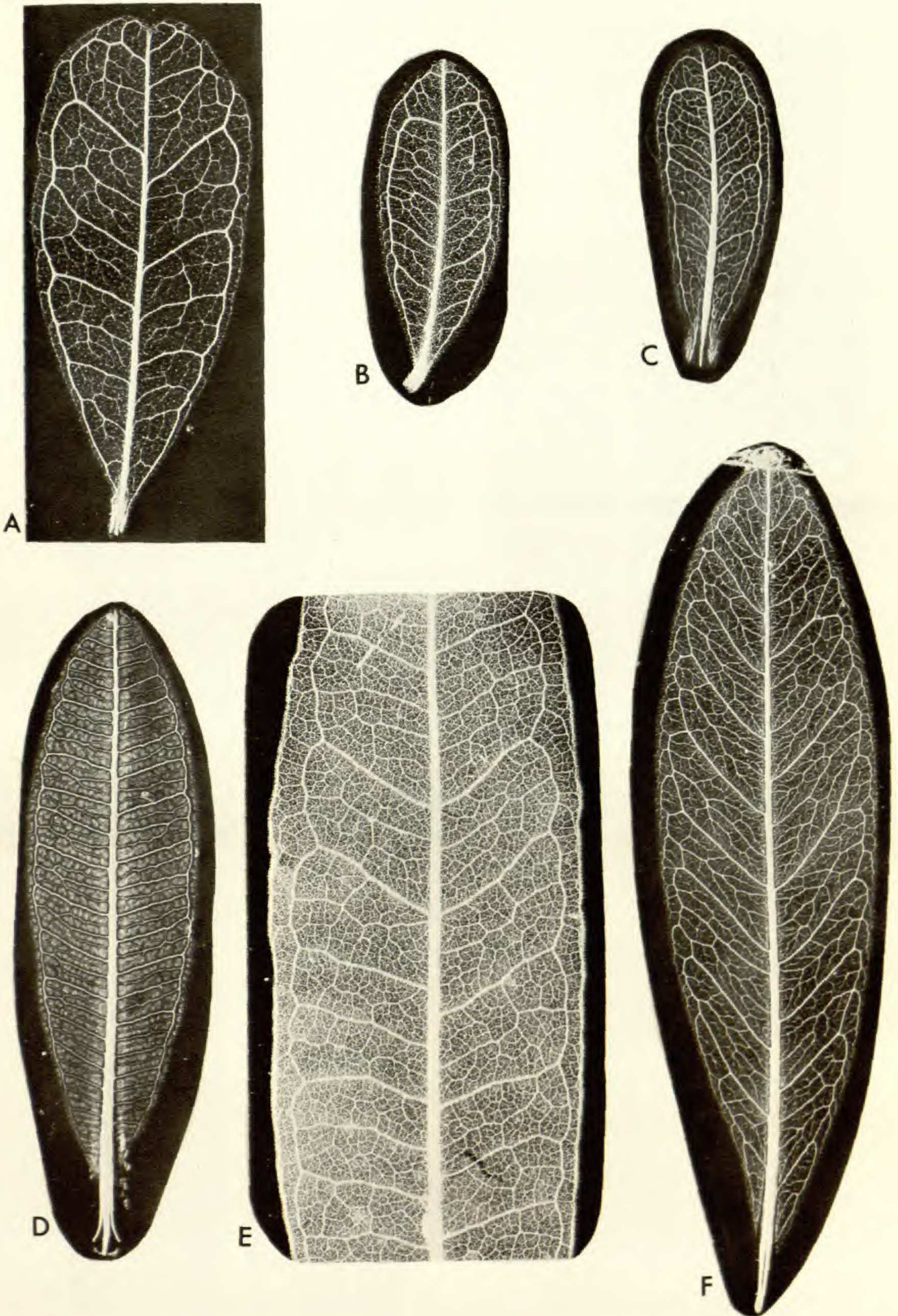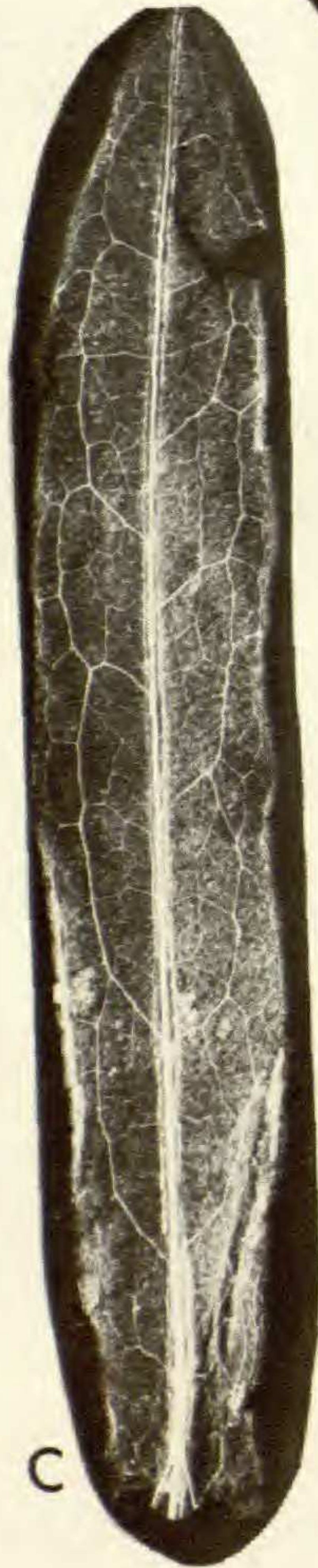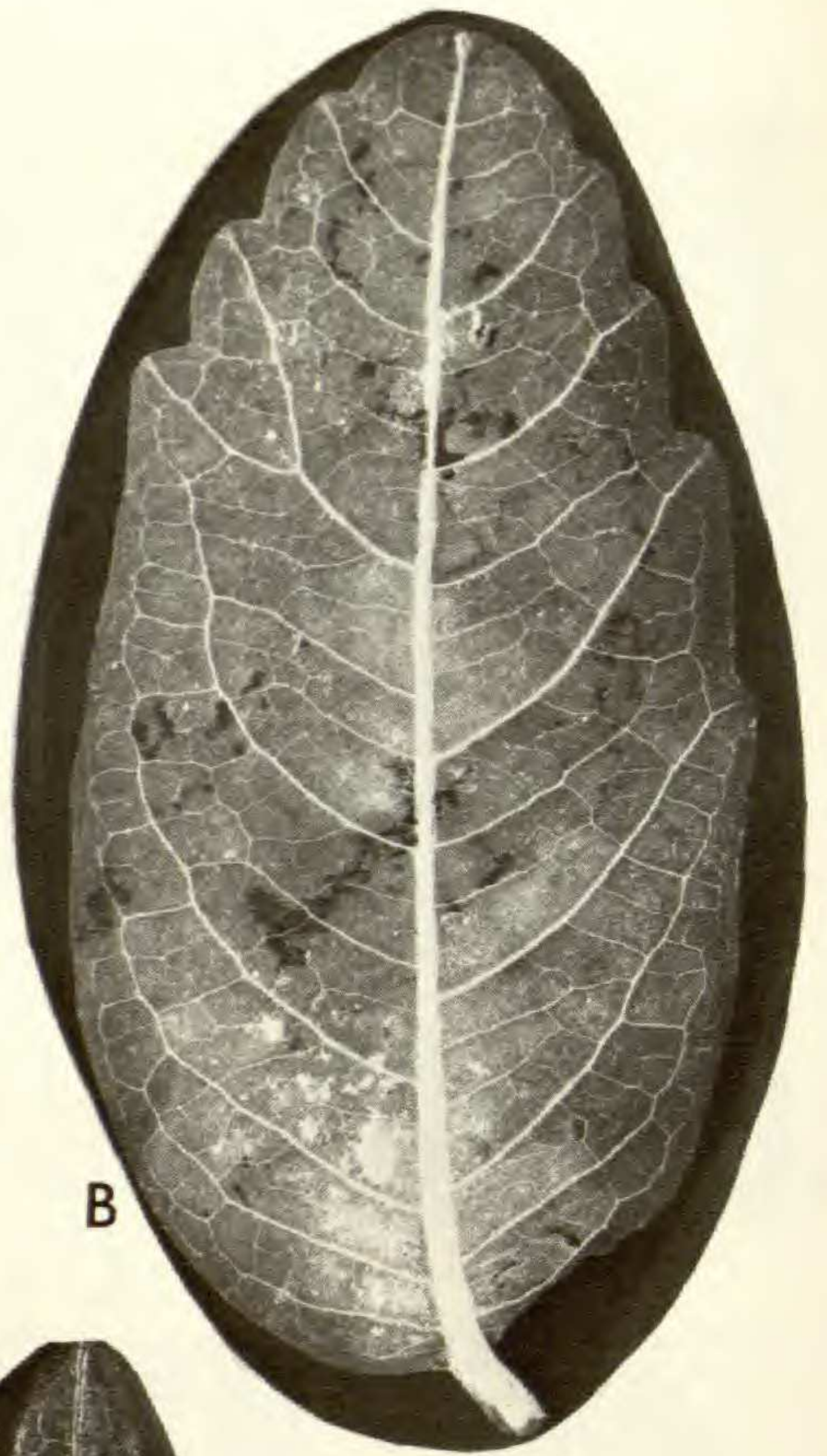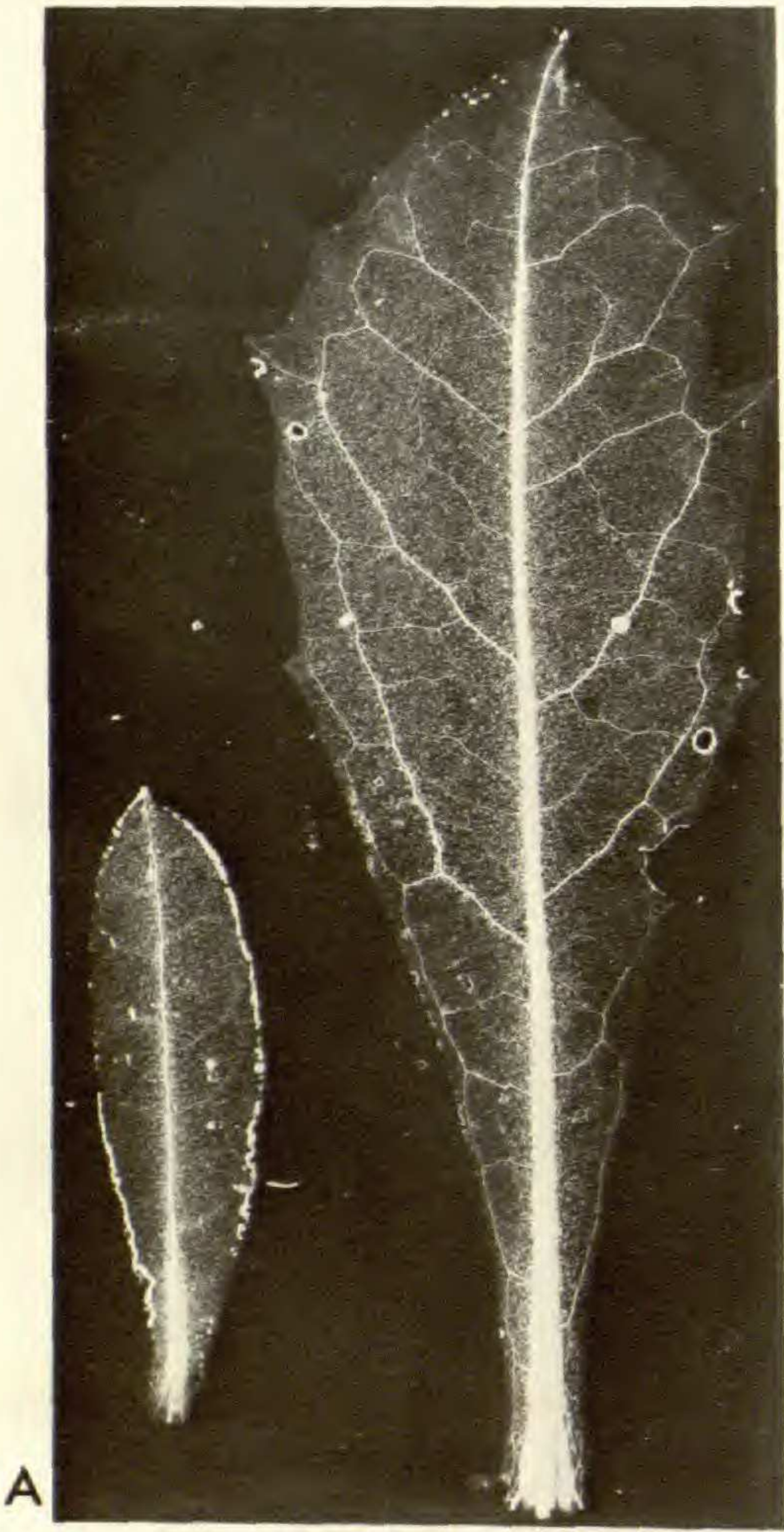
RURY & DICKISON, LEAF VENATION PATTERNS

Plate VII

RURY & DICKISON, LEAF VENATION PATTERNS

RURY & DICKISON, LEAF VENATION PATTERNS

PLATE XI

RURY & DICKISON, LEAF VENATION PATTERNS

RURY & DICKISON, LEAF VENATION PATTERNS